TROPICAL FOREST SUCCESSION: INTEGRATING THEORY AND APPLICATION IN FOREST RESTORATION

By

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First, I dedicate this work to my young son and new love, Ashlin Addison Duncan. I hope forests will return to the degraded lands we leave for his generation.

Second, I dedicate this work to my wife, Virginia Elizabeth Duncan. Ginger's strength and creativity fill each of my days with joy and inspiration.

Finally, I dedicate this work to my late grandmother Irma Ann Jacomine Duncan, and her late sister, Bertha Jacomine Tinerella. I hope the fishing is great, wherever they are.

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Abstract of Dissertation Presented to the Graduate School
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TROPICAL FOREST SUCCESSION: INTEGRATING THEORY AND APPLICATION IN FOREST RESTORATION

By

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During the next century most remaining unprotected tropical forests will be cleared for short-term agriculture or pasture and abandoned. Forests have the natural capacity to regrow after clearing via succession. However, forest succession is often slow or absent on degraded lands, and our limited understanding of succession hinders the design of successful restoration strategies. To address this problem I studied tropical forest succession in Kibale National Park, Uganda, within large sections of forest converted to agriculture then abandoned early last century. These areas became grasslands that persisted until mid-century when timber plantations were established in their place. Unlike grasslands, maturing plantations facilitated native tree and shrub recruitment in their understories. Plantation harvesting began in 1993, and young successional forests growing in their place were the focus of my study. First, I studied the interplay between post-disturbance animal-mediated seed

dispersal and seedling recruitment. This interplay was complex and dependent on the initial onsite availability of resources for succession. Bird seed dispersal had far more impact on plant recruitment than mammal seed dispersal, though few seedlings established relative to numbers of seeds dispersed. Second, I explored the influence of plant-plant interactions (competition and facilitation) on forest succession. Correlative analyses from vegetation surveys suggested interactions between growth forms (shrubs and trees) and size classes (seedlings and saplings) were often strong. However, these interactions were complex and varied among successions. Experimental removal of shrubs or all non-tree vegetation failed to enhance community-wide tree recruitment or survival, though some species responded strongly. Third, I explored restoring natural forests on degraded tropical lands using timber plantations. Overall forest regrowth was dependent on availability of native stems and propagules surviving logging. While logging killed many native stems, it accelerated forest succession relative to that in unlogged plantations. Several attempts to enhance forest succession in logged areas were moderately successful, with some experiments suggesting species-level interventions may be more successful than community-wide interventions. Finally, fire-exclusion appears faster than using plantations to promote forest succession in grasslands. In each of these studies I propose guidelines for managing successions based on my findings.

CHAPTER 1
GENERAL INTRODUCTION

During the next century we will likely see the loss of most remaining unprotected tropical forests. These forests are currently being cleared at a rate of 127,300 km^2 yr^{-1}, logged at a rate of 55,000 km^2 yr^{-1}, and burned as quickly as 30,000 km^2 yr^{-1} (FAO 1999). This problem is widespread, with annual forest loss at 10.5% in Africa, 9.7% in Latin America and the Caribbean, and 6.4% in Asia and Oceania (FAO 1999). Restoration ecologists are already being asked to assist forest regrowth. This may be one of ecology's greatest challenges, for our understanding of how intact tropical forests function is very limited, and our knowledge of how to restore such systems is even more limited (Chazdon 1994).

Fortunately, forests have the natural capacity to grow back after disturbance via the process of succession (Brown & Lugo 1990; Finegan 1996; Holl & Kappelle 1999). This process is shaped by initial and recurrent disturbance intensity, abiotic and biotic resource availability, and changes in biotic interactions through time (Uhl 1982; Uhl et al. 1982; Finegan 1984; Uhl et al. 1988; Finegan 1992; Brown & Lugo 1994). After small-scale or minor disturbances, secondary forest readily establishes, although hundreds of years may pass before a forest resembling the original returns (Ewel 1980; Finegan 1996). However, many anthropogenic disturbances impair the ability of forests to grow back. On such lands, forest succession is often arrested, occurs slowly, or leads to forests compositionally very different from the original (Borhidi 1988; Uhl

et al. 1988; Kuusipalo et al. 1995; Chapman & Chapman 1999). Currently, our limited understanding of forest succession hinders our ability to design successful restoration strategies for such lands (Chazdon 1994). To address this problem, we began studying tropical forest succession in ways we think are relevant to designing successful restoration strategies. This approach, an integration of theory and application, is one we think will be essential for restoration ecology's future success.

We studied forest succession in Kibale National Park, Uganda, within large sections of forest that were converted to agriculture in the early 1900s. These agricultural areas were soon abandoned due to a tsetse fly outbreak and then became dominated by fire-maintained grassland (Osmaston 1959). During the 1950s and 1960s, when Kibale was a forest reserve, many of these grasslands were converted to exotic pine (*Pinus caribeae* and *P. patula*) and cypress (*Cupressus lusitanica*) plantations (Osmaston 1959). During their maturation, these plantations facilitated native tree and shrub recruitment in their understories (Chapman & Chapman 1996; Fimbel & Fimbel 1996). Due to several decades of political instability, plantations went unmanaged and colonizing native trees and shrubs were not cleared. When political stability returned and Kibale became a national park in 1993, officials decided that plantations would be logged and natural forest allowed to grow in their place.

Successional forests developing on logged plantations at Kibale were the focus of our study. Native stem recruitment in pine plantations was greater than was recruitment in cypress plantations (Fimbel & Fimbel 1996). Thus,

succession in logged pine and cypress plantations starts with different initial on-site recruit availabilities. These successional forests are akin to other moderately degraded lands throughout the tropics where successional forests develop after disturbance (e.g., forest conversion to swidden agriculture, clearcut logging, and light pasture use; Uhl et al. 1981; 1982a; 1982b; 1988; Uhl 1987; De Rouw 1993; Toriola et al. 1998; Kammesheidt 1999). Thus, the successional forests at Kibale provided an opportunity to address several issues relevant to understanding forest succession and to developing management applications for restoring forests for biodiversity conservation throughout the tropics.

In Chapter 2 we investigated the influence of plant-animal interactions on the first six years of forest succession. Specifically, we looked at how succession was affected by on-site initial recruit availability (seed bank, seedlings, saplings, coppice, and sprouts) and post-disturbance animal-mediated seed dispersal. Because on-site recruit availability declines with increasing disturbance intensity (Brown & Lugo 1990; 1994), the influence of post-disturbance seed dispersal may increase with the intensity of disturbance (Da Silva et al. 1996; Nepstad et al. 1996). Animal-mediated seed dispersal may be particularly important in successional habitats in the humid tropics, since most trees there are endozoochorous (Howe & Smallwood 1982; Uhl et al. 1988; Chapman et al. 1999). We compared the role of animal-mediated seed dispersal between successional trajectories starting with different levels of recruit availability. This was done by calculating rates of seed dispersal by birds and mammals into

successional habitats of different ages, and quantifying recruitment and growth of animal-dispersed trees and shrubs.

In Chapter 3 we quantified interactions occurring among plants during succession. In particular, we investigated how tree recruitment, growth, and survival were affected by shrubs and other vegetation during the first six years of succession in the logged plantations. Evidence from other tropical successional habitats suggests that non-tree vegetation, especially shrubs, can improve abiotic conditions for tree seedling recruitment (facilitation; Nepstad et al. 1991; Vieira et al. 1994; Aide et al. 1996; Zahawi & Augspurger 1999). Alternatively, such vegetation can inhibit trees through competition (arrested succession; Borhidi 1988; Uhl et al. 1988; Kuusipalo et al. 1995; Holl 1998; Chapman & Chapman 1999; Rogers & Hartemink 2000). Some of these conflicting patterns among studies may be due to variation in strength of facilitative and competitive interactions among sites of varying degradation or successional maturity (Bertness & Callaway 1994; Callaway & Walker 1997). We investigated positive and negative interactions between trees and other vegetation, especially shrubs, with low- and high-recruit availability. We first documented correlations between shrub density and height and tree recruitment and growth. Next, we took an experimental approach and removed shrubs from plots for 16 months to compare tree recruitment, growth, and survival between these and control plots. Finally, we removed all non-tree vegetation for two years from plots and compared tree recruitment, growth, and survival between these and control plots.

In Chapter 4 we examined several ways of managing exotic timber plantations to facilitate forest succession on heavily degraded lands. This potential restoration strategy has gained considerable interest in the last decade (Lugo 1992; 1997; Parrotta 1993; Chapman & Chapman 1996; Parrotta et al. 1997), but little is known about how best to use plantations in restoration (though see Chapman & Chapman 1996; Ashton et al. 1998). We addressed this issue from four perspectives. First, initial on-site recruit availability after disturbance may influence forest succession. Thus, we compared the first six years of succession between successional habitats varying in initial on-site recruit availability. Second, timber harvesting may affect patterns of subsequent forest succession. To quantify these effects, we compared forest succession between logged and unlogged plantations, estimated damage to native stems that occurred during harvest, distinguished between effects of felling timber versus extraction, and examined the influence of disturbance intensity within logged plantations. Third, we examined whether forest succession could be accelerated by planting seedlings, attracting seed-dispersing birds, and vegetation thinning. Finally, we compared several plantation management strategies (e.g., leaving timber unfelled, felling but not extracting timber) to an alternative restoration tool, fire-exclusion.

CHAPTER 2
INITIAL RECRUIT AVAILABILITY VERSUS ANIMAL-MEDIATED SEED DISPERSAL DURING TROPICAL FOREST SUCCESSION

Introduction

Secondary forests are quickly becoming the dominant forest type in the tropics (Brown & Lugo 1990; Nepstad et al. 1996). By the mid-1980s, forests developing after deforestation and agricultural abandonment were < 60-80 years-old occupied 31 percent of the forested tropics (448 million ha; Brown & Lugo 1990). As mature forests continue to disappear (FAO 1999), interest is growing in using secondary forests to provide habitat, forest products, watershed protection, and carbon-dioxide sequestration (Ewel 1986; Finegan 1992; 1996; Brown 1993; Brown & Lugo 1994). While heavily degraded lands (sensu "derelict lands", Brown & Lugo 1994) tend to become dominated by fast-growing plants that arrest succession (e.g., grasses, vines; Brokaw 1983; Borhidi 1988; Uhl et al. 1988; Kuusipalo et al. 1995; Chapman & Chapman 1999), moderately degraded (sensu 'damaged', Brown & Lugo 1994) lands typically have sufficient resources for forest to re-establish in the first decade after disturbance and land abandonment. Forest succession on these moderately degraded lands can be slow, and species composition can differ markedly from the original forest (Uhl et al. 1982a; Finegan 1996). Where the species composition or regrowth rate of successional forest does not meet management goals, intervention may be

needed to speed or redirect succession. However, successful management will require better knowledge of successional processes than is currently available.

Pickett and McDonnell (1989) suggest that site availability, species performance, and species availability are the major factors determining successional trajectories. Species availability has received less attention than have site availability and species performance in tropical forests. Species availability after disturbance is a function of two factors: (1) on-site recruit availability (seed bank, seedlings, saplings, coppice, and sprouts) at the time of disturbance and (2) post-disturbance seed deposition (Pickett & McDonnell 1989). On-site recruit availability tends to decline with increasing disturbance (Brown & Lugo 1990; 1994), and thus, the influence of post-disturbance seed dispersal may also increase with increasing disturbance intensity (Da Silva et al. 1996; Nepstad et al. 1996). Animal-mediated seed dispersal may be especially important for tropical forest regrowth since most trees in the humid tropics are animal-dispersed (Howe & Smallwood 1982; Uhl et al. 1988; Chapman et al. 1999), including most early-successional species (i.e., "pioneers"; Uhl et al. 1981; Howe & Smallwood 1982; Da Silva et al. 1996). Thus, understanding how initial on-site recruit availability and animal-mediated seed dispersal contribute to forest regrowth will be important for predicting growth rates and species composition of secondary forests.

To better understand forest succession on moderately degraded lands, we examined the role of animal-mediated seed dispersal in successional habitats with different initial recruit availabilities. We studied this on logged conifer

plantations surrounded by natural forest in Kibale National Park, Uganda. During their maturation, these plantations fostered the recruitment of native trees and shrubs in their understories (Chapman & Chapman 1996; Fimbel & Fimbel 1996). The two most common plantation types in Kibale differ in native stem recruitment in their understory. Cypress plantations (*Cupressus lusitanica*) have fewer native stems in their understory than do pine plantations (*Pinus caribeae* and *P. patula*). This difference seem caused by dissimilar growth rates and canopy densities of these species (Fimbel & Fimbel 1996). The result is that these plantations types have different on-site recruit densities for succession after logging.

We compared the role of animal-mediated seed dispersal during forest succession between logged pine and cypress plantations, expecting animal-mediated seed dispersal to have most influence on recruitment in logged plantations with lower initial recruit density (logged cypress) than in those with higher initial recruit density (logged pine). To quantify initial on-site recruit availability, we surveyed the soil seed bank and native vegetation in unlogged pine and cypress plantations. We then described plants during the first three years of succession by annually sampling long-term plots in a logged pine and a logged cypress plantation. Older successional communities (4 – 6 years after logging) in pine and cypress plantations were described with one-time surveys. We estimated the numbers of seeds dispersed by birds into these younger and older successional habitats. This entailed capturing birds and calculating seed passage rates based on seeds defecated while detained. We also estimated frugivorous bird densities with bird surveys in logged pine and cypress

plantations. Seed passage rates were related to bird densities to estimate annual seed dispersal rates by birds into the logged plantations. Large mammal seed dispersal rates into younger successional habitats were estimated from dung surveys. With these estimates we evaluated the contribution to recruitment of initial on-site recruit resources versus post-logging animal-mediated seed dispersal.

Methods

Study Site

The study site was located near Makerere University Biological Field Station in Kibale National Park, Uganda (0°34' N, 30°21' E). Kibale encompasses 766 km^2 of mid-elevation moist evergreen forest, swamp forest, papyrus marsh, selectively logged forest, exotic tree plantations, and tall grassland (Kingston 1967; Chapman & Lambert 2000). There are two peaks of rainfall, March to May and September to November. Rainfall averaged 1543 mm yr^{-1} (1903 - 1999), but it has increased in the 1990s (1765 mm yr^{-1}, 1991-1999).

When the forests were first described in 1914, many hilltops there were fire-maintained grasslands dominated by elephant grass (Pennisetum purpureum; Osmaston 1959; Sivell et al. 1996). Archeological evidence, plant community composition, and local folklore suggest these grasslands were former villages and croplands that were abandoned after tsetse fly infestation in the early 1900s (Osmaston 1959; Lang Brown 1962; Sivell et al. 1996). Kibale became a forest reserve in 1932 with timber production a primary mandate. In the 1950s and 1960s, exotic softwoods were planted on many of the grasslands.

During the political instability of the 1970s and 1980s, the trees and shrubs colonizing the plantation understories were not cleared. When Kibale became a national park in 1993, officials decided the plantations would be logged and natural forest allowed to grow in their place. Logging began in 1993 and will likely continue through at least 2002.

Fimbel and Fimbel (1996) found that native trees in unlogged pine plantations at Kibale were taller and twice as dense as in unlogged cypress plantations. Recruitment differences did not appear to be due to soil properties, as no differences in soil chemistry were found between the two plantation types. Landscape positions of the two plantation types appear similar, and documents from the time of planting report no differences in planting sites (Osmaston 1959; Fimbel & Fimbel 1996). Fimbel and Fimbel (1996) hypothesized that pines probably attained canopy closure and suppressed grasses earlier than did cypress, promoting earlier native woody-stem recruitment than in cypress. Also, at plantation maturity, pines allow more light than do cypress into the understory, further aiding stem recruitment in the pine relative to the cypress plantations (Fimbel & Fimbel 1996). Finally, higher densities of native plants in pine understories may have attracted more seed-dispersing animals than did the sparse cypress understories (Fimbel & Fimbel 1996). These reasons probably explain why pine plantations have more initial recruits for forest succession after logging than do cypress plantations.

At maturity, cypress and pine plantations have mean basal areas of 44.4 and 71.3 m^2ha^{-1}, respectively (Fimbel & Fimbel 1996). Cypress trees are shorter

than are pines (23 m versus 33 m, respectively), though mean cypress and pine DBHs are similar (36 cm versus 36 cm, respectively;Fimbel & Fimbel 1996). During plantation harvest, most timber is felled with chainsaws, crushing or damaging many of the native trees and shrubs. Felled stems are rolled or winched to nearby portable sawmills, pitsawing stations, or roads. During the movement of logs, most of the remaining native stems are cut or crushed. The end result is that few stems > 1 m tall remain after logging. However, many seedlings survive logging, and sprouts grow from stumps and roots of many native species. It is our impression that after logging, recruit availability in these plantations is similar to that in moderately degraded areas throughout the tropics (e.g., forest conversion to swidden agriculture, clearcut logging, and light pasture use; Uhl et al. 1981; 1982a; 1982b; 1988; Uhl 1987; De Rouw 1993; Toriola et al. 1998; Kammesheidt 1999).

We studied succession in logged plantations at Kibale from May 1998 - October 2000. Of the ten conifer plantations within Kibale, only four had been harvested when we began our study. Two of these (Butanzi and Lower Camp) had been logged in 1993 – 1994, and represented older successional forest (Table 2-1). Two others (Mikana and Nyamasika) had been logged < 1 year before our study, and represented younger successional forest (Table 2-1). Long-term plots were established in these latter plantations to monitor the first three years of succession. Thus, as is typical for large scale ecosystem manipulations, our design had limited spatial replication. However, it provided a large-scale, unique opportunity to compare the impact of seed dispersal in two

systems differing in initial on-site recruit density, and similar for site history, site conditions, and landscape position.

Soil Seed Bank in Unlogged Plantations

Since seed banks of unlogged plantations may be a source of recruits after logging, we compared soil seed banks between unlogged pine and cypress plantations. Quantities of animal-dispersed seeds in the soil were assessed by germinating seeds from soil samples, sifting soil through a screen, and sorting through leaf litter samples.

To estimate the numbers of shrub and tree seeds that could germinate from plantation soil after logging, two germination trials were conducted. In both trials, soil samples were taken from the only unlogged cypress plantation at the time of study. Soil samples from unlogged pine plantations were taken from a different plantation for each of the trials. Within plantations, sample sites were located by choosing random distances along 80 – 100-m transects, then randomly choosing perpendicular distances (10 – 60 m) on either side of the transect. At these sample sites, a soil subsample without leaf litter (20 x 20 cm wide, 10 cm deep) was collected. Four more soil subsamples were collected 5.65 m away from the first in the four cardinal directions (outlining a 100-m^2 circle). All five subsamples of soil were mixed, and a fifth of each mixture was taken for germination trials.

Germination trials were conducted on raised (ht = 1 m) tables in open areas with no overhanging vegetation. In the first trial, 16 samples (8 from the cypress and 8 from the pine plantation) were monitored from January – June

1999. In the second trial, 22 samples (11 from the cypress and 11 from the pine plantation) were monitored from July – December 1999. Most germinations from soil samples occurred during the first three months, with very few new germinations in the last two months. Each soil sample was spread (1 cm deep) in a table compartment (40 x 100 cm) with raised sides (10 cm) and a sand base on a plastic-lined interior with drainage holes. Both trials were exposed to natural rainfall, but during the second trial, tables were watered regularly to encourage germination and seedling survival. To determine if seeds arrived on the two tables used during the first trial, we monitored a control compartment with plantation soil but no seeds on each table (plantation soil was boiled >30 min to kill seeds; seeds added to boiled soil can germinate; Williams-Linera & Ewel 1984). To determine if sand had viable seeds, we set up a control compartment with only sand on each table of the first trial. The two tables of the second trial shared one boiled-soil control. Since no seeds germinated from the sand controls of the first trial, these controls were not repeated during the second trial.

The seed content of plantation soil was also estimated by sifting soil samples through a wire screen (mesh = 1 mm, few shrubs and trees at Kibale have seeds < 1 mm). Soil samples were collected in the same way as were samples collected for the germination trials, with one fifth of the soil mixture at a sample site taken for sifting. Soil samples (n = 40) were taken from three pine plantations; fewer cypress samples were taken (n = 26) due to limited available area in the only unlogged cypress plantation.

We also estimated seeds in leaf litter in the unlogged cypress plantation and an adjacent unlogged pine plantation. Fifteen sample sites in each plantation were chosen following the same procedure described for soil sampling. At each sample site, five litter subsamples (each 20 x 20 cm) were collected and mixed in the same way as soil subsamples were collected. One fifth of each litter mixture was then carefully examined for seeds. Seeds from soil and litter samples were identified from a reference collection. Morphotypes of unknown seeds were considered separate species.

Vegetation Surveys

Vegetation was surveyed in unlogged plantations to further quantify recruit density prior to logging, and in logged plantations to quantify successional forest development. During vegetation surveys in both unlogged and logged plantations, we described trees and shrubs $\geq$ 1 m tall (species, number, height) in non-overlapping 20 – 25-m^2 plots randomly distributed among transects that were evenly distributed throughout the entire plantation, and separated by $\geq$ 10 m (see Table 2-1 for summary of plot sample sizes and shapes for each surveyed plantation). Smaller tree and shrub stems (ht $\leq$ 0.25 m) were described (species, number) in subplots (area = 4 m^2). Throughout, we refer to these taller stems (ht $\geq$ 1 m) as 'saplings', though many shrub saplings were reproductively mature, and we refer to these smaller stems (ht $\leq$ 0.25 m) 'seedlings' though they may have no longer been dependent on seed reserves or may have been root sprouts. Plants were identified using identification manuals by Eggeling and Dale (1952), Pohill (1952), Hamilton (1991), and Katende et al. (1995). From these

texts and our own observations, we classified trees and shrubs as animal-dispersed or non-animal-dispersed (e.g., wind-dispersed). Because the focus of our study was animal-mediated seed dispersal, we excluded all non-animal-dispersed species from analyses (animal-dispersed species were on average 60% and 85% of shrubs and trees (respectively) in the logged plantations, and 89% and 59% of shrubs and trees (respectively) in the unlogged plantations.

While Fimbel and Fimbel (1996) described differences in native stem recruitment below unlogged pine and cypress plantations at Kibale, we wanted to confirm these patterns at the time of our study, and describe smaller stems not included in their surveys. We sampled the only remaining unlogged cypress plantation and an adjacent unlogged pine plantation, thus controlling for site history and landscape position. In each plantation, plots were placed by choosing random distances along a 100-m transect, then choosing a random distance from 1 - 60 m perpendicular to the transect (Table 2-1). The open understory of the unlogged plantations allowed us to use circular plots, which were faster to survey than are rectangular plots that we used in surveys of logged plantations (Table 2-1).

In one recently logged cypress and one recently logged pine plantation, vegetation was sampled within one year of logging (~ 4 and ~ 9 months after logging, respectively). In both plantations, these same plots were resampled one and two years later. These plots were square, and randomly placed along parallel transects (10 m apart) that covered the entire logged area (Table 2-1). No plots included in analyses of early successional habitats (1 – 3 years) were

on heavily disturbed areas within plantations (roads or portable sawmill and pitsawing sites).

For the oldest successional areas (4 - 6 years after logging), vegetation in two logged cypress and one logged pine plantation was sampled once (Table 2-1). The two logged cypress plantations were then pooled for comparisons to the logged pine plantation. Plot locations were chosen as in the recently logged plantations. We used rectangular plots in these areas to make sampling of the dense vegetation easier. In these older successional habitats some former pitsawing stations may have been included in analyses since these areas were hard to identify.

We determined the proportion of seedlings (from seed) versus sprouts (from roots or stems buried during logging) by destructively sampling small trees and shrubs in logged areas. Sampling in a younger successional habitat was done in a pine plantation logged 3 – 11 months previously; sampling in an older successional habitat was done in a cypress plantation logged 6 years previously. In the younger successional habitat, we sampled 17 plots (each 4 m^2) distributed every 5 m along a randomly placed transect. In each plot we dug up all stems that would have been classified as seedlings (ht $\leq$ 0.25 m) during vegetation surveys. We determined whether their roots were connected to buried stems or roots from adjacent plants (sprouts), or they were true seedlings. To increase our sample size in the younger successional habitat, we also sampled stems in three randomly placed 50 x 2-m belt transects. In the older successional habitat, we sampled stems in one randomly placed 50 x 2 m-belt transect.

Bird Surveys

To describe densities of seed-dispersing birds using successional areas, we surveyed birds in plots in 1-, 2-, and 5 - 6-year-old logged pine and cypress plantations during May-August 1999 (see Table 2-2 for summary of survey methods). Plots were evenly spaced within available habitat of these six successional areas, and were > 10 m from roads. Distance between plots varied depending on available habitat; flagging tape demarcated plot edges (Table 2-2). In the small 1- and 2-year-old successional forests in the logged cypress plantation, rectangular plots were used since more of these could be set up than could circular plots.

We conducted point count surveys of these plots between 0700 – 1030 hr. The 4 min surveys were preceded by a minute after our arrival for birds to resume natural activities. Birds flushed when we entered plots were included in surveys. During surveys we stood in the center of circular plots and at the edge of rectangular plots, since the vegetation in the latter plots was very low (1.0 - 1.5 m). Subsequent sightings of a species during a survey were not counted unless we knew birds were new individuals. We did not count birds flying over or through the plot because they were not likely dispersing seeds into the plot (Charles-Dominique 1986). Each plot was sampled five times, no more than twice each day during the period of June – August 1999. We haphazardly switched sampling order among plots each new sampling day, and we sampled in all weather except rain. Birds were identified with the aid of 10 x 42 binoculars and Williams and Arlott (1980), van Perlo (1995), and Zimmerman et al. (1996).

We classified species as seed dispersers if they were ever observed eating fruit, observed defecating/regurgitating seeds, or known from the literature to eat fruit. Only seed-dispersing birds were included in our analyses.

Mistnetting Surveys and Seed Rain Estimates

To quantify the numbers of seeds dispersed by birds into successional habitats, we mistnetted birds in a cypress plantation 4 years after logging. Our estimates of seed rain into other successional habitats was based on passage rates of shrub and tree seeds found in this 4-year-old successional forest. Mistnetting birds in 1 – 3-year-old successional habitats was deemed impractical because nets would have been visible to birds in the low vegetation of these habitats. We do not know how well seed dispersal in this one plantation reflects seed dispersal in the other successional habitats. However, all of the successional habitats we studied are surrounded by forests sharing similar site histories, landscape positions, and species compositions (seed sources). Given these similarities and that we only make inferences about seed rain at the growth form level, we are satisfied that seed rain from mistnetted birds in the 4-year-old successional forest generally reflects the composition of seed growth forms dispersed into the other habitats.

We netted every other week in May - October 1998, February - May 1999, and August - December 1999 on 12 randomly chosen netting sites. At each site a narrow trail accommodated a mistnet (length = 4.6 or 9.1 m; mesh size = 1.9 cm). To capture canopy and gap dwelling species that use this area but usually evaded nets in the successional forest understory, we netted in six locations on

the edges of small (100 m^2) experimental clearings in the plantation where non-tree vegetation had been removed (Chapman et al. in press). Netting was done between 0645 and 1300 hr in all weather except rain; nets were checked every 30 minutes. To collect seeds, we placed each bird in a 8 liter bucket with a cloth cover. Birds were kept for ~ 40 - 60 minutes, enough time for most of their seeds to be defecated or regurgitated (Levey 1986; Graham et al. 1995). Birds were then released, and seeds were collected from buckets and identified. To recover seeds defecated while birds were in the net, we collected seeds from black plastic sheets placed below nets.

To estimate seed-defecation rates for birds, we calculated the mean number of shrub and tree seeds collected for all birds kept $\geq$ 40 min. These numbers were divided by 0.67 hr (40 min), the time when the number of seeds collected from captive birds peaked. Rates (seeds $bird^{-1}$ $hour^{-1}$) were then multiplied by the seed disperser densities (birds ha^{-1}) from the point count surveys to approximate hourly rates of seed defecation into each successional area (seeds ha^{-1} hr^{-1}). We then scaled this hourly rate to a daily defecation rate. However, because our bird-density estimates were from hours when birds were most active in the successional habitats, we could not assume the calculated defecation rate represented seed dispersal throughout the entire day (seed-dispersing birds in these habitats spend much of their time in adjacent undisturbed forest). Thus, we multiplied the hourly seed-defecation rates by 5 hr day^{-1}, our estimation of the number of hours per day when seed-dispersing bird activity in the plantations was greatest. This probably yielded conservative

estimations of daily defecation rates since birds are present in lower densities during the other seven hours of daylight. For successional habitats less than one year old, the daily seed rain rate (seeds ha^{-1} day^{-1}) was multiplied by the estimated number of days since logging to estimate number of seeds dispersed into each plantation between logging and the time of vegetation surveys. For older successional habitats the daily seed rain rate was scaled to one year (seeds ha^{-1} yr^{-1}). To relate this estimate to seedling density from vegetation plots, we converted seed-defecation rates to seeds m^{-2} yr^{-1}.

Mammalian Dung Surveys

Baboons (*Papio anubis*), elephants (*Loxodonta africana*), civets (*Civettictis civetta*), and chimpanzees (*Pan troglodytes*) occasionally visit recently cleared plantations and may disperse seed species not typically dispersed by birds into these areas. We surveyed logged areas for large mammal dung and tracked success of dispersed seeds. Monthly surveys were conducted in 1 – 3-year-old cypress (Mikana) and pine (Nyamasika) successional habitats (August 1998 – September 2000, and August 1998 - June 1999, respectively). Surveys in the logged cypress plantation were occasionally suspended when logging resumed nearby (November 1998 – February 1999). In both plantations a different set of 4-m-wide transects was surveyed monthly, totaling 500 m and 550 m per month in the logged cypress and pine plantations, respectively. Transect sets were resampled every seventh month in the logged pine plantation and every third month in the smaller logged cypress plantation. Transects walked during monthly surveys were separated by 60 - 40 m. We stopped censusing

these two sites when vegetation became too dense to easily find dung. For each monthly survey we pooled all transects and calculated density of seeds found in dung (seeds m^{-2}). Densities were averaged among all surveys, and the average was used to estimate yearly seed input by large mammals (seeds m^{-2} $year^{-1}$). To do this, we assumed that seeds found during a survey represented two weeks of seed rain. This seemed reasonable since mammal dung in these habitats often dried quickly (deterring secondary seed dispersal by most dung beetles, but not rodents) and remained intact for several weeks. In addition, when we varied the time period we assumed that a survey represented by several weeks, our conclusions about the role of mammalian seed dispersal were unaffected.

When dung was found, seeds were counted, identified, left in place in dung, and the site marked. To record seedling establishment, during the first year we visited all dung sites every 6 mo after the first survey in each plantation. By April 1999 it was clear few seedlings were establishing from defecation sites in heavily disturbed areas (trails, roads, offcut piles, and sawdust piles) or on logs and stumps. To augment sample size of dung in less disturbed areas, dung found in heavily disturbed locations was moved to the ground in nearby vegetation beginning May 1999. In January 2000 we began surveying seedlings every 2 months to increase the probability of detecting germination.

Because number of defecations found on transects was low, we conducted monthly haphazard surveys in the successional habitats until September 2000 to better quantify the seeds dispersed by large mammals. In addition, monthly haphazard surveys were begun in January - September 2000

in three other recently logged pine plantations. Seedling survivorship was not followed in these latter sites, and data from haphazard surveys were not used to estimate seed dispersal rates into the successional habitats.

Statistical Analyses

We used non-parametric analyses for most comparisons because nearly all data were strongly zero-skewed (e.g., soil seed bank, vegetation survey, and bird survey data). Accordingly, we present medians to describe data. We also present means to facilitate comparisons with other studies in which parametric analyses were used. Statistical analyses were performed with SPSS 10.0.5 for Windows (1999). Significance was set at $P \leq 0.05$, though marginally nonsignificant results at $P \leq 0.10$ are noted as "trends".

Results

Soil Seed Bank in Unlogged Plantations

Density and species richness of animal-dispersed tree and shrub seeds in soil and leaf litter samples did not differ between unlogged pine and cypress plantations (Table 2-3). There was a trend for greater tree species richness in pine than in cypress litter samples, and a trend for greater shrub seed density and species richness in pine than in cypress soil samples. In the first germination trial, no differences in density or species richness of germinated animal-dispersed trees and shrubs were found between plantations (Table 2-3). In the second germination trial, animal-dispersed tree seed density and species

richness were significantly greater in pine than in cypress soil samples; shrub seed density and species richness were similar between plantations. No animal-dispersed tree or shrub seeds germinated from any controls during either germination trial.

Vegetation Surveys

Unlogged pine and cypress plantations had similar density and species richness of animal-dispersed tree seedlings (Fig 1, 2). But for most other stem categories, the pine plantation had significantly greater density and species richness, and animal-dispersed shrub and tree saplings were significantly taller in the pine than in cypress plantation (Table 2-4). These results confirmed that logged pine and cypress plantations have high and low initial recruit availabilities, respectively.

When the logged pine and cypress plantations were compared within a year of logging, there were significantly more animal-dispersed tree saplings in pine plots. Shrub sapling and tree seedling densities between successional habitats were similar (Fig. 1). There was a trend for more shrub seedlings in cypress than in pine plots. Tree seedling and shrub sapling species richness between successional habitats were similar, but there were significantly more tree sapling species in the logged pine plantation, and significantly more shrub seedling species in the logged cypress plantation (Fig. 2). Tree saplings were significantly taller in the logged pine than in the logged cypress plantation, but shrub saplings were of similar heights in the successional habitats (Table 2-4).

In younger successional habitats 44% of destructively sampled shrub "seedlings" were actually sprouts from stems buried during logging or roots, and 23% of destructively sampled tree "seedlings" were sprouts (Table 2-5). In the older successsion, 90% and 100% of shrub and tree "seedlings" were actually seedlings, not sprouts. Thus, seedling surveys overestimated number of stems recruiting directly from seed, though less so in older successional habitats.

From two to six years after logging, tree seedling densities and species richnesses in pine and cypress plantations declined, then dramatically increased (Fig. 1, 2). At no time did tree seedling densities and species richnesses differ between the logged pine and cypress plantations. During this period, tree sapling density, species richness, and height increased in both logged plantation types. These three stem variables in the logged cypress plantation became similar to those in the logged pine plantation (Table 2-4; Fig. 1, 2). Between two to six years after logging, shrub seedling density and species richness became significantly greater in the logged cypress than in the logged pine plantation (Fig. 1, 2). Shrub sapling density, species richness, and height varied from being similar or slightly significantly different between the two successional habitats over this period (Table 2-4; Fig. 1, 2).

Bird Surveys

The density of seed-dispersing birds was greatest 6 years after logging in the logged cypress plantation and 2 years after logging in the logged pine plantation (Table 2-6). Variation in bird density among point counts within plantations was high, but some trends emerged. Bird density was similar

between logged pine and logged cypress plantations during the first year, but during the second year the logged pine plantation had significantly greater density than did the logged cypress plantation. At 5 – 6 years after logging, there was a trend for greater bird density in the logged cypress than in the logged pine plantation.

Mistnetting Surveys and Seed Rain Estimates

During 72 days of netting, we captured 470 birds of 51 species. Of these, 325 birds were of the 20 species known to disperse seeds. A total of 11,685 seeds were collected of 46 plant species. The most abundant growth forms of collected seeds were shrubs (73%) and trees (21%), followed by vines (5%).

On average, seed-dispersing birds defecated into buckets 39 seeds $bird^{-1}$ (SD = 99, n = 277 captures). Seed-defecation rates of tree and shrub seeds were 8.5 and 28.4 seeds $bird^{-1}$ $hour^{-1}$, respectively. Estimated rates of seed rain into all successional habitats greatly exceeded median seedling densities of animal-dispersed species (Table 2-7), especially in the younger successional habitats where many stems classified as seedlings were actually sprouts (Table 2-5). Thus, plant colonization at the community level in the successional habitats appears to be more establishment-limited than it is dispersal-limited.

Mammalian Dung Surveys

Sixty-nine mammal defecations containing 9,088 seeds were found in recently logged plantations during transect and haphazard surveys. Most defecations were from baboons (75%) and elephants (17%), with a few

defecations from civets (6.5%) and chimpanzees (1.5%; Table 2-8). Only baboon dung was found in logged pine plantations. Civets dispersed far more tree seeds per defecation than did any of the other species, but all of these seeds were *Diospyros abyssinica* (n = 2750 seeds), a mid-successional tree, or *Bridelia micrantha* (n = 2475 seeds), an early-successional tree. Among all mammals, most seeds found were tree seeds (63%), followed by herbs (27%); shrubs contributed < 1% of all seeds found (Table 2-8). Eleven and six total defecations were found in cypress and pine transect surveys, respectively (Table 2-8; χ^2= 0.9, P = 0.332). The estimated yearly density of tree and shrub seeds dispersed by mammals into successional habitats was very low relative to seed rain from birds (Table 2-7).

Nearly half of all defecation sites were in locations where seedlings were expected to have very low chances of establishing (heavily disturbed sites; Table 2-8). But among transect surveys, only 28% (n = 5) of defecations were found in heavily disturbed sites. Many dung sites (30%) were destroyed by subsequent logging activity before the end of the experiment; seedling survival data for these sites were not analyzed.

When we considered only dung sites that were not disturbed by subsequent logging activities and were in favorable locations for establishment (Table 2-9), very few seedlings survived to the end of the study, totaling 0.3% of all seeds found in dung. Because some small seeds were probably undetected in dung, this procedure probably overestimated the proportion of seedlings emerging from seeds. The only tree seedlings to survive to the end of the

experiment had established within four months of the final survey (10 *Bridelia micrantha*, 2 *Kigelia africana*, 1 *Myrianthus holstii*); with more time, many of these would probably die (Table 2-9). All shrub seedlings found were of seeds undetected when dung was found (many shrub species have small seeds), suggesting we underestimated shrub seed dispersal (Table 2-9). No shrub seedlings found prior to the last survey survived to the end of the study. The number of vine and herb seedlings found was 4% of vine and herb seeds found in dung, and seedlings surviving to the end of the experiment were only 0.3% of these seeds.

The four defecations in heavily disturbed locations that were undisturbed by subsequent logging activities had 392 seeds (including 3 tree and 39 shrub seeds); only 23 seedlings (1 herb, 2 vines, and 20 shrubs) were found among these sites, and none survived to the end of the study.

Discussion

The Influence of Seed Dispersal on Succession

We draw four major conclusions about the influence of seed dispersal on succession in these moderately disturbed habitats. First, in all successional habitats we studied, numbers of seeds dispersed by animals appeared to far exceed number of recruited seedlings. Thus, at the community level, establishment limitations seem to drive recruitment patterns in these successional habitats. Second, in all successional habitats studied, the influence

of post-disturbance seed dispersal on seedling recruitment varied over time, suggesting fluctuating recruit availabilities and/or establishment conditions.

Our third conclusion is post-disturbance animal-mediated seed dispersal seemed to contribute many of tree seedlings recruiting during both periods of high seedling recruitment. Sprouts were only ~ 20% of stems classified as tree seedlings during the first year of succession. Of the 80% that were actual seedlings, our prelogging surveys suggested very few were seedlings that had survived logging. Instead, most of these seedlings probably recruited from the prelogging seed bank and post-disturbance seed dispersal. The second pulse in tree seedling recruitment at 4 – 6 years after logging included very few sprouts. Of the seedlings, very few probably originated from the prelogging seed bank, or were seedlings established before logging. Thus, animal-mediated seed dispersal seemed to drive most tree seedling recruitment in the years following disturbance, especially later in succession.

Seedling recruitment declined sharply after the first year despite the fact that many early-successional plants were fruiting and frugivorous bird densities were high. One explanation for this decline may be the exhaustion of the soil seed bank and root reserves for sprouting. In addition, most dispersed seeds were probably shade-intolerant early-successional species unable to establish in dense understory established by this time. Alternatively, the paucity in seedling recruitment may have resulted from high levels of seed or seedling predation. In any case, the pulse in seedling recruitment at 4 – 6 years after logging was probably due to an improvement in seedling establishment conditions, though

there may have also been greater arrival of shade-tolerant mid- and late-successional seedling species able to establish in the understory. These results suggest that variation in post-dispersal processes will make it difficult to predict seedling recruitment rates based on estimates of seed disperser and/or fruit-producing plant densities (Vieira et al. 1994; Nepstad et al. 1996; Duncan & Duncan 2000).

Our fourth conclusion is that birds were far more important than were mammals as seed dispersers into the early successional habitats. Densities of bird-dispersed seeds exceeded those of mammal-dispersed seeds by several orders of magnitude, and for three mammal species many dispersed seeds were herbs and vines, not trees. While several of the tree seeds dispersed by mammals were large-seeded late-successional species not usually dispersed by birds (*Mimusops bagshawei*, *Monodora myristica*, *Uvariopsis congensis*), none of these germinated and survived to the end of the study. Similarly, among other mammal-dispersed species, very few seedlings germinated and survived. While large mammals had little apparent influence on succession as seed dispersers, their contribution to species recruitment may be greater later in succession.

These patterns suggest that post-disturbance seed dispersal especially by birds is important to succession in moderately degraded habitats such as those found after plantation logging at Kibale. However, effects of seed dispersal are mediated by strong establishment limitations that allow temporally distinct pulses of seedling establishment. It is against these patterns that we can consider the

role of seed dispersal between the two successional habitats differing in initial on-site recruit availability.

Seed Dispersal Versus Initial Recruit Density in Successional Habitats

We examined the role of post-disturbance animal-mediated seed dispersal in forest succession on moderately degraded sites differing in initial recruit availability. We hypothesized that successional habitats with low initial recruit densities (logged cypress) would be influenced more by seed dispersal than would successional habitats with high initial recruit densities (logged pine). Our findings confirmed our predictions, but processes involved were more complex than was expected, suggesting that predicting the impact of seed dispersal on moderately degraded lands will be difficult.

Logged pine plantations started succession with more on-site recruits than did logged cypress plantations. However, this disparity disappeared with time, and by 4 - 6 years after logging most indices of woody stem recruitment (density, species richness, height) in the logged cypress plantation equaled or surpassed those in the logged pine plantation. This convergence in forest structure and species richness began when many early-successional shrubs recruited during the first year in the logged cypress plantation. Shrub seed density in the prelogging cypress seed bank was low, suggesting that root sprouting or post-disturbance seed dispersal were the source of recruitment. While up to half of shrub seedlings in the first year of succession may have actually been root sprouts, one of the most important shrubs attracting frugivorous birds into this successional habitat, *Hoslundia opposita*, seems to not sprout frequently (1 of 8

seedling-sized stems found was a sprout). Thus, bird dispersal of shrub seeds seemed to play an important role in shrub recruitment in logged cypress plantations, while mammals dispersed very few shrub seeds. These newly recruited shrubs and those surviving logging produced fruits that attracted seed-dispersing birds in the first year. These birds probably dispersed tree and shrub seeds responsible for the second pulse in seedling recruitment seen at 4 -6 years in the older successional habitat. Through this indirect path, tree recruitment and growth in the logged cypress plantation matched that in the logged pine plantation.

Succession in the logged pine plantations seemed to follow a different trajectory. Unlike the logged cypress plantation, the logged pine plantation had little shrub recruitment during the first years, probably due to low shrub seed density in prelogging seed bank and low density of shrub saplings before logging. However, many seed-dispersing birds were attracted to the high density of early-successional fruiting trees that recruited after logging, and probably dispersed seeds for the seedling recruitment pulse at 4 - 6 years after logging.

We found that successional habitats can converge in terms of stem density, species richness, and height among moderately degraded sites differing in initial recruit availability. This may have occurred because successional habitats starting with lower initial recruit densities had more space for colonization than did successional habitats with greater initial recruit densities. The time needed for successional convergence among sites will probably depend on initial recruit availability, and seed dispersal and establishment rates.

In our system, convergence between the successional habitats for stem density and species richness appears to be rapid (< 10 years), probably because recruitment was not dispersal limited. Successional convergence in forest structure and species richness may take longer among sites varying in seed dispersal input due to distance from seed source and/or abundance of seed dispersers, or among sites where initial recruit availability is more divergent than were the two successional habitats we studied here. While not considered in our study, successional convergence in species composition may also take a long time.

From the literature it is not clear how frequently nor at what time scale successional convergence occurs on sites varying in recruit availability. Many successional studies in the tropics compare a chronosequence of a single disturbance type to mature forest to estimate recovery time (Saldarriaga et al. 1988; Dalling & Denslow 1998; Zahawi & Augspurger 1999; Denslow & Guzman 2000). While widely recognized that tropical forest recovery varies with disturbance intensity, and hence initial recruit availability (Brown & Lugo 1994), there are few quantitative comparisons of succession on sites differing in disturbance intensity. Studies contrasting disturbance types usually compare moderately and heavily degraded sites, and rarely is recruitment from post-disturbance seed dispersal compared to recruitment from other sources. Uhl et al. (1982a) compared forest regrowth after cutting, cutting and burning, and bulldozer clearing in Venezuela. They estimated that biomass would match that in undisturbed forest in 100 years in cut and cut-and-burned treatments, and

1000 years in the bulldozed treatment. Uhl et al. (1988) studied forest regeneration on abandoned pastures of light, moderate, and heavy degradation in the Brazilian Amazon and found large differences in biomass, tree species richness, or tree density among the treatment types after eight years of succession. In Nigeria, Adedeji (1984) compared recruitment on deforested sites where felled vegetation was burned or just removed, but the successional habitats had not converged at two years. In Ivory Coast, De Rouw (1994) studied succession in abandoned upland rice fields where the forest had been recently cut and the slash burned to varying degrees before planting. Post-disturbance seed dispersal had more impact in heavily burned than in lightly burned clearcuts. Aide et al. (1996) found that the structure (tree density, basal area, species richness, species diversity) of secondary forests in Puerto Rico resembled that of undisturbed forest after 40 years of succession. More comparative and, especially, experimental studies are needed to determine whether and when convergence occurs among different successional trajectories. This information will be important for determining which disturbed areas under management are in most need of intervention (e.g., those where convergence with more rapid successional trajectories is not expected).

The Management Implications of Successional Complexity

Predicting species recruitment rates and compositions during succession will be useful for identifying successional habitats most needing intervention, and determining when during succession intervention will be most successful. We found that recruitment patterns can be complex, suggesting that accurately

predicting regeneration patterns will be difficult. In light of such complexities and the four major findings of our study, we offer suggestions for managing successional habitats. First, we found that community-level recruitment was not limited by seed dispersal into successional habitats. This was an encouraging finding given that seed dispersal is a frequent impediment to forest succession in heavily degraded systems (Nepstad et al. 1991; Holl 1999). The high abundance of seed sources and dispersers in our study was partially due to the successional habitats being near forests, though several important seed-dispersing birds were not forest species (e.g., common bulbuls, *Pycnonotus barbatus*). Where recruitment from seed rain is low, managers could try to improve understory establishment conditions. Other interventions may be needed in moderately degraded habitats where seed rain is low. One strategy is directly distributing seeds into successional habitats (Sun et al. 1995; Pinard et al. 1996; Hau 1997; Chapman & Chapman 1999). Or, managers could attract dispersers and supply seed sources by planting fast-growing fruit-producing trees in or near the site (Tucker & Murphy 1997). Erecting artificial perches to attract seed dispersing birds may be useful in some situations, but establishment conditions below such perches are often poor (Holl 1998a; Toh et al. 1999). Because it will be difficult to predict with much certainty the success of such interventions, it would be wise to employ multiple strategies for achieving increased recruitment.

Second, we found temporal variation in seedling recruitment during succession. This presents a major challenge to managers distributing seeds or seedlings into successional habitats. For example, to establish early-

successional shade-intolerant species, it may be important to distribute seeds or plant seedlings very early in succession before the understory becomes dominated by herbs and vines. Or, if seed or seedling predation is a major source of propagule mortality, managers may wish to plant seedlings that are old enough to withstand herbivory. In general, it will be important for the distribution of propagules into successional habitats to coincide with the availability of favorable establishment conditions. Since it may be difficult to predict when favorable establishment conditions occur, natural seedling recruitment patterns could be monitored to identify when favorable recruitment periods begin.

Third, seed-dispersing birds were very important to early forest succession, while seed-dispersing mammals were not. Thus, if forest succession is limited by seed arrival, perhaps attempts to increase seed rain should initially be focused on birds (e.g., planting fast-maturing animal-dispersed shrubs or trees). Attracting mammals to successional areas may be more advantageous later in succession when establishment conditions for large-seeded mammal-dispersed species have improved.

Finally, we found convergence in structure and species richness of moderately degraded successional habitats with different initial recruit availabilities. While this may suggest less intervention is needed where initial recruit availability is lower, other studies have indicated that convergence may be slow or may never occur due to colonization limitations (e.g., arrested successions). Thus, it will be important to monitor the progress of forest succession to determine when intervention is needed to reach management

goals. We still do not understand many of the processes important in forest succession on degraded lands. And, few published evaluations of management strategies exist. It is critical that researchers continue investigating successional process, and managers conduct and publish well-designed experiments to determine which interventions are most successful.

Table 2-1. The successional areas in Kibale where vegetation surveys were conducted, and time since logging when surveyed. * indicate long-term plots surveyed annually. ‡ indicate two logged cypress plantations of similar ages combined for analysis. The Mikana and Butanzi localities had both pine and cypress plantations, with portions of the latter harvested at different times.

Age of successional habitat	Locality	Plot shape, size, and seedling plot placement	N plots sampled
Cypress plantations			
unlogged	Mikana	Circular, area = 25 m^2, center	15
<1 year after logging *	Mikana	Square, 25 m^2, corner	24
2 years after logging *	Mikana	Square, 25 m^2, corner	22
3 years after logging *	Mikana	Square, 25 m^2, corner	22
4 years after logging ‡	Lower Camp	Rectangular, 10x2 m, center	27
5 years after logging ‡	Butanzi	Rectangular, 10x2 m, center	26
Pine plantations			
unlogged	Mikana	Circular, area = 25 m^2, center	15
<1 year after logging *	Nyamasika	Square, 25 m^2, corner	25
2 years after logging *	Nyamasika	Square, 25 m^2, corner	24
3 years after logging *	Nyamasika	Square, 25 m^2, corner	25
5 - 6 years after logging	Butanzi	Rectangular, 10x2 m, center	30

Table 2-2. Design of frugivorous bird surveys of plots in successional habitats of different ages on logged pine and cypress plantations.

Age of successional habitat	# of plots	Point count shape and area	Minimum distance to adjacent point counts
Cypress plantations			
1 year after logging	9	rectangle, area = 425 - 707 m^2	> 20 m
2 years after logging	10	rectangle, area = 480 - 750 m^2	> 20 m
6 years after logging	10	circle, area = 708 m^2	> 25 m
Pine plantations			
1 year after logging	10	circle, area = 708 m^2	> 30 m
2 years after logging	10	circle, area = 708 m^2	> 20 m
5 - 6 years after logging	10	circle, area = 708 m^2	10 m for n = 6 0 m for n = 4

Table 2-3. Median (top number) and mean (bottom number ± SD) seeds m^{-2} and species m^{-2} of animal-dispersed tree and shrub species from soil seed bank and leaf litter surveys in several unlogged pine and one unlogged cypress plantations. P values are results of Mann-Whitney comparisons of samples between plantation types.

Sampling method	Trees			Shrubs		
	Pine	Cypress	P value	Pine	Cypress	P value
Seed density						
Soil sifting	0 3 (8)	0 3 (8)	0.802	0 3 (8)	0 0 (0)	0.068
Litter sorting	25 20 (25)	0 68 (244)	0.116	0 2 (7)	0 0 (0)	0.317
1998 Germination trial	13 31 (59)	13 68 (113)	0.732	0 0 (0)	0 3 (9)	0.317
1999 Germination trial	150 123 (121)	0 0 (0)	0.002	0 9 (17)	0 5 (15)	0.329
Species richness						
Soil sifting	0 3 (8)	0 2 (7)	0.788	0 3 (8)	0 0 (0)	0.068
Litter sorting	25 15 (16)	0 5 (10)	0.055	0 2 (7)	0 0 (0)	0.317
1998 Germination trial	1 1 (1)	1 1 (1)	1.000	0 0 (0)	0 0 (0)	0.317
1999 Germination trial	50 30 (25)	0 0 (0)	0.002	0 7 (12)	0 2 (8)	0.280

Table 2-4. Median (top number) and mean (bottom number ± SD) height of animal-dispersed tree and shrub saplings (ht ≥ 1.0 m) in unlogged and logged plantations. P values are from comparisons of stem heights between pine and cypress plantations (Mann-Whitney test).

Succession age	Trees			Shrubs		
	Pine	Cypress	P value	Pine	Cypress	P value
Unlogged	2.8 2.8 (2.8)	0 0.9 (1.2)	< 0.001	1.9 2.2 (0.8)	1.0 0.9 (1.0)	< 0.001
1 year	1.5 1.8 (1.1)	0 0.6 (0.7)	< 0.001	1.2 1.1 (0.7)	1.3 0.9 (0.7)	0.566
2 year	2.3 2.5 (0.7)	1.3 1.2 (0.8)	< 0.001	1.6 1.8 (0.5)	1.9 1.9 (0.7)	0.187
3 year	3.7 3.9 (1.2)	1.6 1.5 (0.9)	< 0.001	2.2 2.2 (0.9)	1.9 2.1 (0.6)	0.396
4 - 6 years	2.8 3.4 (1.9)	2.8 2.7 (1.3)	0.216	3.0 3.0 (1.2)	2.6 2.5 (0.8)	0.034

Table 2-5. Frequencies of seedlings versus sprouts (from roots or stems buried during logging) for stems ≤ 0.25 m tall in logged plantations of different ages. All such stems were classified as seedlings during vegetation surveys.

Sampling sites	Total species	Total stems	% sprouts	% seedlings
Younger successional habitats (< 1 yr old)				
Shrubs	17	271	43.9	56.1
Trees	12	101	22.8	77.2
Older successional habitats (6 yr old)				
Shrubs	9	62	9.7	90.3
Trees	8	32	0	100

Table 2-6. Medians, means (in brackets), and ranges (in parentheses) of seed-dispersing bird densities (birds ha^{-1}) in point count areas in successional forests of different ages in logged pine and cypress plantations. P values are from Mann-Whitney comparisons of the bird densities between the two succession types.

Successional age	Pine	Cypress	P value
Bird Densities			
Year 1	2.8 [4.0] (0 - 17.0)	12.1 [14.3] (0 - 45.5)	0.121
Year 2	24.0 [28.6] (2.8 - 70.7)	8.7 [10.4] (0 - 28.6)	0.041
Year 4 - 6	15.6 [21.2] (0 - 56.6)	24.0 [36.2] (14.0 - 84.9)	0.095

Table 2-7. Estimated yearly seed rain from birds and mammals and median seedling densities (ht $\leq$ 0.25 m) in successional habitats of different ages on logged pine and cypress plantations. Seed rain for the first year was calculated for the time between logging and the vegetation surveys that quantified seedling density. Mammal seed rain was pooled for year one and two.

Successional habitat and variable	Year 1	Year 2	Year 4 - 6
Trees			
Logged pine plantation			
Bird seed rain (seeds m^{-2} $year^{-1}$)	9.2	66.2	49.1
Mammal seed rain (seeds m^{-2} $year^{-1}$)		0.27	-
Seedling density (seedlings m^{-2})	0.8	0	1.3
Logged cypress plantation			
Bird seed rain (seeds m^{-2} $year^{-1}$)	10.9	24.1	83.9
Mammal seed rain (seeds m^{-2} $year^{-1}$)		0.01	-
Seedling density (seedlings m^{-2})	0.6	0	1
Shrubs			
Logged pine plantation			
Bird seed rain (seeds m^{-2} $year^{-1}$)	30.8	222.0	164.8
Mammal seed rain (seeds m^{-2} $year^{-1}$)		< 0.01	-
Seedling density (seedlings m^{-2})	0	0	0
Logged cypress plantation			
Bird seed rain (seeds m^{-2} $year^{-1}$)	36.5	81.0	281.3
Mammal seed rain (seeds m^{-2} $year^{-1}$)		0.01	-
Seedling density (seedlings m^{-2})	0.3	0	0.5

Table 2-8. Number of defecations and mean (± SD) seeds per defecation for mammal dung found in logged pine and cypress plantations. Number of defecations is divided between the two survey types (haphazard and transect), and the disturbance intensity of defecation sites (highly disturbed and moderately disturbed sites). Eleven and 31 transect and haphazard surveys were completed in the logged pine plantations, respectively; 14 transect and haphazard surveys were completed in the logged cypress plantation.

Disperser species	Number of defecations				Mean seeds defecation^{-1}	Mean seeds growth form^{-1} defecation^{-1}					
	Haphazard		Transect								
	High	Moderate	High	Moderate		Trees	Shrub	Vines	Herbs	Unknown	Crops
Logged cypress plantation											
Baboon	3	6	3	5	69	<1 (1)	<1 (2)	20 (49)	47 (93)	1 (3)	<1 (2)
Elephant	6	3	1	2	8	3 (4)	<1 (1)	5 (6)	0	0	0
Civet	3	1	0	0	1596	1306 (728)	2 (4)	94 (75)	194 (200)	0	0
Chimpanzee	0	1	0	0	81	44	0	0	37	0	0
Logged pine plantations											
Baboon	17	12	1	5	37	11 (26)	1 (4)	2 (7)	23 (36)	<1 (2)	0

Table 2-9. Numbers of seeds and seedlings found, and seedlings surviving to the end of the study from mammal dung in two early successional habitats (< 3 years old). All data included here are from dung on moderately disturbed sites monitored to the end of the study (see text for details). For the number of seedlings found, parenthetical numbers are additional seedlings of species undetected when dung was discovered. For the number of seedlings surviving, parenthetical numbers are the subset of surviving seedlings discovered on the last survey.

Growth form and variable	Successional area		
	Cypress	Pine	Total
Trees			
# seeds found	4749	209	4958
# seedlings found	20	0	20
	(4)		(4)
# seedlings surviving	12	0	12
	(1)		(1)
Shrubs			
# seeds found	5	20	25
# seedlings found	0	0	0
	(1)	(20)	(21)
# seedlings surviving	0	0	1
			(1)
Vines, herbs, and unknown seeds			
# seeds found	1676	301	1977
# seedlings found	58	0	58
	(16)	(5)	(21)
# seedlings surviving	4	1	5
	(3)		(3)

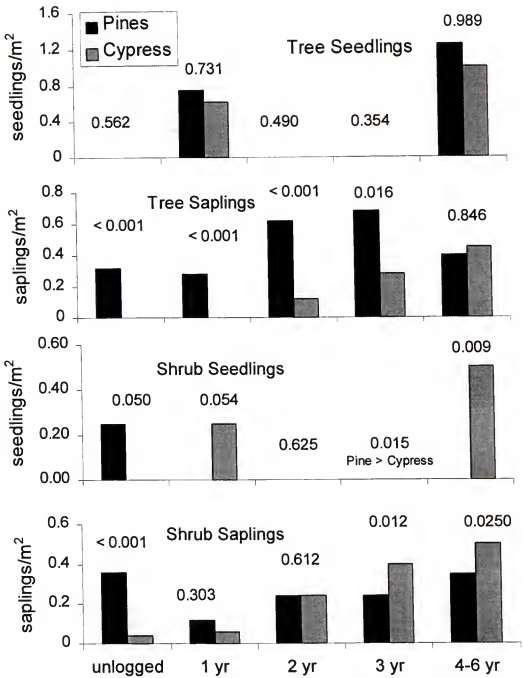

Figure 1. Median stem densities for animal-dispersed tree and shrub species in pine and cypress plantations before and after logging. P values indicate results of Mann-Whitney contrasts between logged pine and cypress plantations at each successional age.

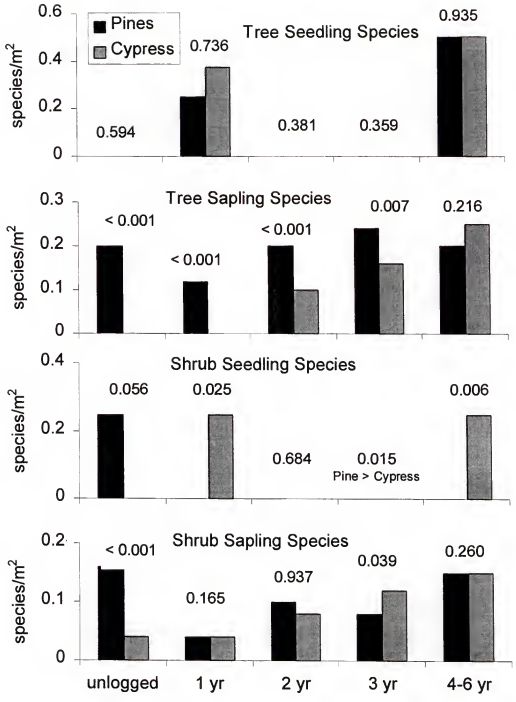

Figure 2. Median species richness for animal-dispersed tree and shrub species in pine and cypress plantations before and after logging. P values indicate results of Mann-Whitney contrasts between logged pine and cypress plantations at each successional age.

CHAPTER 3
MANAGEMENT IMPLICATIONS OF TREE-SHRUB INTERACTIONS DURING EARLY FOREST SUCCESSION ON DEGRADED TROPICAL LANDS

Introduction

During the 1990s, tropical lands were deforested at a rate of 127,300 km^2 yr^{-1} (FAO 1999). Restoring forests on these lands will be one of the greatest challenges for restoration ecologists in this century (Brown & Lugo 1994). These forests will be important for providing extractable resources (e.g., timber), ecosystem services (e.g., soil and watershed protection), and habitat for animal and plant populations (Ewel 1986; Finegan 1992; Brown 1993; Brown & Lugo 1994; Finegan 1996). However, restoring forests on degraded lands requires an understanding of the processes of forest regrowth. In particular, managers need to know when and where intervention will be necessary to initiate or assist forest succession, and how to manage developing forests to meet management goals.

One important process affecting forest succession is the interaction between trees and other plants of the successional community. On severely degraded lands, fast-growing non-tree species (often vines, ferns, grasses) can prevent or slow tree invasion (arrested succession; Borhidi 1988; Uhl et al. 1988; Kuusipalo et al. 1995; Chapman & Chapman 1999). While shrubs often quickly invade degraded habitats, their role in forest succession is unclear. For example, they may compete with trees for limited resources (e.g., light, soil nutrients) and, thus, slow forest regrowth (Putz & Canham 1992; Berkowitz et al. 1995; Holl

1998b; Rogers & Hartemink 2000). However, because abiotic conditions of degraded lands are often unfavorable for tree seedling recruitment, shrubs may act as "nurse crops" by buffering harsh abiotic conditions, thus facilitating tree recruitment (Nepstad et al. 1991; Vieira et al. 1994; Aide et al. 1996; Zahawi & Augspurger 1999). For example, shrubs may provide shade, reducing temperature, soil moisture loss, and grass density (Vieira et al. 1994; Li & Wilson 1998; Raffaele & Veblen 1998). Because the harshness of abiotic conditions increases with increasing site degradation, shrubs may facilitate tree recruitment in heavily degraded systems and hinder tree recruitment in less degraded systems (Bertness & Callaway 1994; Callaway & Walker 1997). Or, shrubs could initially facilitate tree seedling recruitment in early-successional habitats and later compete with these trees as they mature (Callaway & Walker 1997).

We investigated the effects of shrubs and other non-tree vegetation (vines, grasses, herbs) on tree recruitment and growth during the first six years of natural forest succession on logged timber plantations in Kibale National Park, Uganda. First, we looked for correlations between shrub density and height and tree recruitment and growth. Second, we removed only shrubs from vegetation plots in an early-successional habitat for sixteen months, and compared subsequent tree recruitment and growth between these and control plots. Third, we removed all non-tree vegetation for two years from plots in early-successional habitats and compared tree recruitment and growth between these and control plots. Because the initial availability of on-site recruits after disturbance may affect interactions between trees and other vegetation during the first years of

succession, we compared positive and negative interactions between trees and other vegetation types in two successional habitats differing in initial on-site recruit availability. We interpret our results in light of designing interventions to promote forest succession.

Methods

Study Site

We studied forest succession in unlogged and logged exotic softwood plantations near Makerere University Biological Field Station (0°34' N, 30°21' E) in the Kibale National Park, Uganda. Kibale is dominated by moist evergreen forest; average elevation is ~ 1500 m, and rainfall averages 1543 mm yr^{-1} (1903 - 1999), though it increased to 1765 mm yr^{-1} in recent years (1991-1999). Plantations were established during the 1950s and 1960s on grasslands (*Pennisetum purpureum*) that were in a state of fire-maintained arrested succession (Osmaston 1959; Sivell et al. 1996). These grasslands were present on hilltops when the area was first described in 1914 (Osmaston 1959). Evidence suggests the grasslands were forested before conversion to agriculture, but were abandoned when tsetse flies infested the area in the early 1900s (Osmaston 1959; Sivell et al. 1996). Plantations were unmanaged as they matured, and many species of native trees and shrubs colonized their understories. Logging of plantations began in 1993 when Kibale became a national park. Current plans are to allow natural forest to re-establish.

Pine (*Pinus caribeae* and *P. patula*) and cypress (*Cupressus lusitanica*) were the two main timber species planted at Kibale. Native trees in unlogged plantation understories are taller and more dense in pine than in cypress (Fimbel & Fimbel 1996). These differences do not appear to result from soil properties, landscape position, or timing of planting (Osmaston 1959; Fimbel & Fimbel 1996). Instead, differences in native stem recruitment are probably due to differential timber growth rates and understory light availabilities between pine and cypress (Fimbel & Fimbel 1996). These differences between plantations in preharvest stem density translated into differences in on-site recruit availability for forest succession after plantations were harvested. Both habitats can be considered moderately degraded, as opposed to heavily degraded habitats where unassisted forest succession proceeds very slowly. From May 1998 to October 2000, we studied forest succession in a chronosequence of pine and cypress plantations logged between 1993 – 1998.

Tree and Shrub Interactions

We examined correlational evidence for interactions between shrubs and trees before logging and during the first six years of succession in logged plantations. For each plantation type (pine and cypress), we sampled one unlogged plantation, one recently logged plantation (1 – 3 years after logging), and one plantation 5 – 6 years after logging. These were the only available pairs of similarly-aged unlogged or logged pine and cypress plantations at Kibale. As is typical for large scale ecosystem manipulations, our design had limited spatial replication. However, this system provided a large scale, unique opportunity to

study plant interactions between two systems differing in initial on-site recruit availability, but sharing similar landscape positions, site histories, and site conditions.

Fimbel and Fimbel (1996) described differences in native stem recruitment below unlogged pine and cypress plantations at Kibale. To confirm these patterns at the time of our study and describe smaller stems not included in their study, we conducted vegetation surveys in the only remaining unlogged cypress plantation, and an adjacent unlogged pine plantation (thus controlling for landscape position and site history). Within each plantation, 15 non-overlapping vegetation plots were positioned by choosing random distances along a 100-m transect, then choosing a random distance 1 - 60 m perpendicular to the transect. The open understory of the unlogged plantations allowed us to use 25-m^2 circular plots, which were faster to survey than in the rectangular plots we used in surveys of logged plantations. In plots in unlogged plantations, we measured density, species richness, and height of all shrub and tree stems $\geq$ 1 m tall. We refer to these stems as "saplings", though many shrub saplings were reproductively mature. Smaller stems (ht $\leq$ 0.25 m) and intermediate stems (0.26 – 0.99 m tall), were sampled in circular 4-m^2 subplots. We refer to the smaller stems as "seedlings," and the intermediate-sized stems as "large seedlings", though stems of either group may have no longer been dependent on seed reserves (especially large seedlings) or may have been root sprouts. Plant identification was based on Eggeling (1952), Pohill (1952), Hamilton (1991), and Katende (1995).

Vegetation during the first three years of succession was surveyed with long-term vegetation plots (set up July – August 1998) in one recently logged pine plantation and one recently logged cypress plantation (four and nine months after logging, respectively). Twenty-five plots were randomly placed (though non-overlapping) in each plantation along parallel transects (10 m apart) that covered the entire logged area. All of these plots were in moderately disturbed areas, as opposed to heavily disturbed areas (e.g., roads, former portable sawmill or pitsawing sites). These 5 x 5-m plots were surveyed when plots were set up, then again at two and three years after logging. Stems < 1 m tall were sampled in 2 x 2 m subplots. Vegetation was quantified as was done in the unlogged plantation. The number of these early-successional plots sampled after the first year varied since some plots were lost or destroyed by logging trucks in transit to other plantations. At two years after logging, 22 and 24 long-term plots were resurveyed in the cypress and pine plantations, respectively. At three years after logging, 21 and 25 long-term plots were re-surveyed in the cypress and pine plantations, respectively. Many of the stems classified as seedlings in the first year after logging (44% and 23% of shrub and tree "seedlings", respectively) were actually sprouts from roots or coppice from stems buried during logging (Duncan & Chapman in prep a).

We also surveyed the oldest successional habitats in logged plantations at Kibale (5 - 6 yrs after logging). The vegetation of one logged cypress and one logged pine cypress plantation was sampled once (n = 28 and 30 plots, respectively). Plot positioning and sampling followed that of the more recently

logged plantations. We used 2 x 10-m plots in these areas to ease sampling of the dense vegetation; stems < 1 m tall were sampled in 2 x 2 m subplots. Some former heavily disturbed areas may have been included in these surveys since these areas were hard to identify.

To look for patterns of how shrubs affected recruitment, survival, and growth of trees, we looked for correlations of stem density, species richness, and height between shrub saplings and both tree saplings and seedlings. We also looked for correlations between shrub saplings and shrub seedlings. Finally, since trees may also affect recruitment, we looked for correlations between tree saplings and tree and shrub seedlings. Here and throughout this study we use non-parametric analyses because our data were often highly zero-skewed. When medians are presented, we also provide means to aid comparisons with other studies where parametric analyses were used.

Shrub-Removal Experiment

To examine the effect shrubs have on tree recruitment, in June 1999 we removed shrubs from 19 plots in the only recently logged plantation available at the time; 19 control plots were also established. All plots were 5 x 5 m, a size that seemed sufficient to affect interactions among the small (ht < 1.6 m) trees and shrubs in this early stage of succession. In removal plots, larger shrubs (height ~ > 0.5 m) were cut at the base, while smaller shrubs were pulled from the ground. Subsequent shrub removal occurred every three months. Great care was taken during shrub removal to avoid trampling all other vegetation. Immediately after the first clearing and at the end of the experiment 16 months

later, tree and shrub saplings were identified, counted, and their heights measured in removal and control plots. The final survey also included stems < 1 m tall in 2 x 2-m subplots. Subplots were placed in the center of larger plots to reduce shading from stems outside the larger plot. Since vines are often abundant in early-successional habitats and may respond to shrub removal more quickly than do trees, we ranked vine coverage on a 0 – 4 scale (0 = no vines, 1 = 1 – 25% coverage, 2 = 26 - 50%, 3 = 51 – 75%, 4 = 76 – 100%).

Community-level tree density, species richness, and height were compared between the removal and control plots. At the guild level, we compared the removal and control plots for the numbers of trees belonging to either early-successional or mid- and late-successional categories. These designations were based on Eggeling (1952), Pohill (1952), Hamilton (1991), and Katende (1995) and our own observations. Late-successional species were uncommon in successional habitats at Kibale and were pooled with mid-successional species for comparisons. At the species level we compared the responses of individual tree species between removal and control treatments.

Vegetation-Removal Experiment

To determine how trees are affected by interactions with the entire plant community, we experimentally removed all non-tree vegetation (shrubs, vines, grasses, herbs) from plots in early-successional habitats. Plots were 5 x 5 m, with 2 x 2-m subplots placed in the center for sampling smaller stems (ht < 1.0 m). These vegetation-removal plots were established within a year after logging (August – September 1998) in the same cypress and pine plantations where

undisturbed succession was monitored with long-term plots (n = 22 and 20 plots in logged pine and cypress, respectively). Sample sizes differed between plantations because some plots were destroyed by logging trucks. Approximately every four months, plots were cleared of all non-tree vegetation. Shrubs were removed as in the shrub-removal experiment, while all other vegetation was pulled from the ground. During the first removal, all remnant branches of plantation timber species were removed. Care was taken to not disturb tree stems during vegetation removal. Plots were surveyed as in the shrub-removal experiment when first cleared, at one year, and at two years after initial clearing. Smaller stems (ht < 1.0 m) were quantified only during the final survey. Vegetation-removal plots were compared to long-term plots located within the same logged plantation. Aspects of this experiment were analyzed by Duncan and Chapman (in prep c) as a potential management tool for enhancing forest succession.

Statistics

Most statistical analyses were performed with SPSS 10.0.5 for Windows (1999), and the VassarStats: Website for Statistical Computation (Lowry 2000). Significance was set at $P \leq 0.05$, though nonsignificant differences at $P \leq 0.10$ are noted as "trends".

Results

Tree and Shrub Interactions

In the logged cypress plantation, all tree and shrub sapling variables prior to logging and one year after logging were significantly positively related to one another (e.g., shrub sapling density and tree sapling height; Figs. 1, 2). However, two years after logging no significant relationships between tree and shrub sapling variables remained. In the third and fifth years after logging, relationships between tree and shrub sapling variables became difficult to interpret. For example, tree sapling density and shrub sapling height were nonsignificantly negatively related in the third year of succession, but then were significantly positively related in the fifth year of succession (Fig. 2).

In the logged pine plantation, few significant relationships existed between tree and shrub sapling variables before logging (Figs. 3, 4). All tree sapling variables were nonsignificantly negatively related to shrub sapling density and nonsignificantly positively related to shrub sapling height. After logging, tree sapling density and species richness became nonsignificantly positively related to shrub sapling density. Tree sapling height was usually negatively related to shrub sapling density, although this relationship was significant only 5 – 6 years after logging (Fig. 3). Tree sapling density and species richness were often significantly positively related to shrub sapling height. Tree and shrub sapling height correlations showed no consistent trends (Fig. 4).

In logged cypress plantations, tree and shrub seedling variables 2 – 3 years after logging switched from negative to positive relationships (significantly or nonsignificantly) with shrub sapling height and tree sapling density (Figs. 2, 5).

The same switch was seen with shrub seedling variables and shrub sapling density (Fig. 1) and to a limited extent between tree seedling variables and tree sapling height (Fig. 5). Tree seedling variables were generally negatively related (significantly or nonsignificantly) to shrub sapling density (Fig. 1), and shrub seedling variables were generally negatively related (significantly or nonsignificantly) to tree sapling height (Fig. 5).

In logged pine plantations, relationships of tree or shrub seedling variables to shrub sapling variables across the successional ages showed few consistent trends through time (Figs. 3, 4). Directions of relationships were usually consistent within a year, but directional trends typically switched between years. Tree seedling variables were positively related (significantly or nonsignificantly) with tree sapling density through time, but the relationship between tree seedling variables and tree sapling height showed no consistent trends (Fig. 6). The relationship between shrub seedling variables and tree sapling density shifted from negative to positive through time (significantly or nonsignificantly); shrub seedling variables were consistently negatively related (significantly or nonsignificantly) with tree sapling height (Fig. 6).

Shrub-Removal Experiment

Tree sapling density, species richness, and height were initially similar between control and shrub-removal plots (Table 3-1). By the end of the experiment, shrub removal resulted in lower shrub sapling density, species richness, and height in removal than in control plots (Table 3-1). However, shrub removal did not affect shrub stems < 1 m tall (probably due to resprouting).

At the end of the experiment, no differences existed between control and removal plots in densities of tree saplings or stems < 1 m tall (Table 3-1). There was a trend for greater vine cover in removal than in control plots (Mann-Whitney test, P = 0.091). No differences existed in the number of early- versus mid- and late-successional tree stems < 1 m tall (Chi-square, P = 0.740) or saplings (Chi-square, P = 0.238). At the species level, only *Diospyros abyssinica* had enough stems < 1 m tall for comparison (n $\geq$ 10 for Chi-square tests) between treatments; there was a trend for more *D. abyssinica* stems in control than in removal plots (n = 15 and 6 stems, respectively; Chi-square, P = 0.081). For saplings, *Trema orientalis* had more stems in removal than in control plots, but all other species with sufficient sample sizes for comparison had similar numbers between treatments (Table 3-2). When sapling height was compared between treatments for species with sufficient sample sizes (n $\geq$ 6 stems per treatment for t tests), *T. orientalis* saplings were taller in removal than in control plots (Table 3-2). There was a trend for taller *Celtis africana* saplings in control than in removal plots (Table 3-2).

Vegetation-Removal Plots

After one year of vegetation removal in the logged cypress plantation, tree saplings were taller in removal than in control plots, but tree sapling density and species richness were similar between treatments (Fig. 7). In the pine plantation, tree saplings were of similar height and density, but species richness was greater in control plots (Fig. 7). By the second year in the logged cypress plantation, no differences existed between in the removal and control plots for tree sapling

height, density, or species richness in either the logged pine or logged cypress plantations (Fig. 7). Tree seedling density and species richness did not differ between removal and control plots in the logged pine plantation (Mann-Whitney test, P = 0.481 and 0.448, respectively) or the logged cypress plantation (Mann-Whitney test, P = 0.197 and 0.127, respectively).

In the pine plantation, sapling density of early- versus mid- and late-successional species was dependent on treatment, with greater numbers of early-successional species in removal than in control plots, and greater numbers of mid- and late-successional species in control than in removal plots (Chi-square, P = 0.001). Stems < 1 m tall showed no significant interaction between treatment and successional status (Chi-square, P = 0.256). In the logged cypress plantation, interactions between treatment and successional status were not significant for numbers of saplings and stems < 1 m tall (Chi-square, P = 0.841 and 0.752, respectively).

When treatments were compared at the species level, most tree species showing differences in sapling numbers had more stems in control plots than in removal plots, regardless of which logged plantation was considered (Table 3-3). The exception was *T. orientalis* in the logged pine plantation. In contrast, among stems < 1 m tall, species differing between treatments usually had more stems in removal than in control plots (Table 3-3).

After two years in the logged cypress plantation, most tree sapling species were of similar height between treatments (Table 3-3). *Bridelia micrantha* saplings were taller in control than in removal plots, and there was a trend for

taller *T. orientalis* saplings in removal than in control plots. In the logged pine plantation, most species were of similar height between treatments, though *T. orientalis* saplings were shorter in removal than in control plots.

Discussion

Tree and Shrub Interactions

Our analyses of successional habitats in logged plantations suggested shrub-tree interactions can be highly variable. Despite this variation several trends emerged. First, the relationship between any two stem categories usually changed in direction and strength through time. This suggests that simple characterizations of relationships (e.g., positive or negative, facilitative or competitive) between stem categories will be difficult. Second, few similarities in relationships among stem categories existed when the two habitats having high and low initial recruit densities were compared. This suggests initial recruit availability has a strong effect on the interactions between stem categories during the first years of forest succession. Third, within either successional habitat, stems of the same size class (seedlings or saplings) generally had similar relationships to one another, suggesting that interactions between stems of different sizes or ages can be stronger than are interactions between growth forms. For example, tree and shrub sapling variables were usually positively related to one another (though not always significantly), suggesting they had facilitative relationships, or they responded similarly to a common factor (e.g., disturbance intensity during logging).

The strongest trend suggesting competitive and facilitative interactions was in logged cypress plantations where most shrub and tree seedling variables had initially negative then positive relationships to sapling variables (shrub and tree). This could suggest a switch from competitive to facilitative interactions between seedlings and saplings as the successional forest developed. In contrast, the likelihood of facilitation and competition is expected to decrease and increase during succession, respectively, as abiotic harshness declines (e.g., increasing shade provides lower temperatures, greater soil moisture;Bertness & Callaway 1994; Callaway & Walker 1997). One explanation for these unexpected patterns is the first seedlings were shade-intolerant species unable to establish or survive below taller stems. Alternatively, facilitation was absent during the first year because many plants considered "seedlings" were actually root sprouts or coppice from buried stems (Duncan & Chapman in prep a), recruit sources less likely to benefit from shade. Or, these apparent interactions between seedlings and saplings could have been driven by responses to common factors. These alternative hypotheses illustrate that correlative patterns can only suggest, not confirm, the presence of competitive or facilitative interactions. Carefully designed experiments are needed to determine what causes such patterns. However, such experiments may demand time and resources not readily available to most managers, thus illustrating the need for researchers to pursue these questions.

Others have also found complex interactions between growth forms during forest successsion. Li et al. (1999) found that shrubs inhibited tree growth, but

enhanced soil nutrients in older subtropical successional forests. Berkowitz et al. (1995) found that non-tree vegetation, including shrubs, inhibited tree seedling growth, but facilitated tree seedling recruitment. Walker (1994) found a similar relationship between ferns and tree seedlings on landslides. Factors like tree and non-tree stem density and resource availability are likely to interact to produce complex patterns within and among successions. For example, Berkowitz et al. (1995) found that tree growth was slow on low-resource sites, but was also slow on high-resource sites due to competition with other plants. Complex relationships between facilitation and competition seem to be common among plant communities (Callaway & Walker 1997; Holmgren et al. 1997), thus underscoring the need for managers to carefully consider whether encouraging or removing non-tree vegetation will enhance forest succession.

Vegetation- and Shrub-Removal Experiments

While our correlative analyses suggested facilitative and competitive relationships between shrubs and trees, and saplings and seedlings, these patterns could also have been affected by plant responses to other variables. Thus, we hoped an experimental approach would more clearly illustrate the interactions between trees and shrubs.

There was little indication that removal of shrubs or all non-tree vegetation strongly affected community-level tree recruitment or growth in our experiments. Removal of non-tree vegetation only temporarily enhanced tree growth in the logged cypress plantation and reduced tree species richness in the logged pine plantation. One explanation for absence of a strong removal effect may be that

competitive/facilitative interactions were weak during this period of succession. Alternatively, these interactions may not have been apparent if resources were still relatively unlimited (e.g., light). Or, shrubs and non-tree vegetation facilitated and limited tree recruitment and growth to similar magnitudes.

There was some indication of differences between early and mid- to late-successional species in response to shrub or non-tree vegetation removal in the pine plantation. While these results suggested that non-tree vegetation inhibited early-successional species and benefited mid- and late-successional species, no patterns were found among successional guilds in the other experiments. Thus, using successional status to predict tree responses to thinning at the community level may not be successful. However, several seedling species responded significantly (positively or negatively) to vegetation-removal treatments, suggesting a species-level approach to designing vegetation manipulation treatments may be advantageous.

Others have found that removal of non-tree vegetation increases tree recruitment and/or growth in tropical successions. Holl (1998b) found that shrubs and grasses inhibited tree seedling growth through both above- and below-ground competition. Guariguata (1999) found that thinning of nearby vegetation helped trees grow in a 4.5-year-old successional forest. Li et al. (1999) found that shrub removal increased tree biomass only in forests older than 25 years, and had no effect on tree density across a chronosequence. In Indonesia, Otsamo (1998) found that removal of planted nurse crop trees improved growth of tree saplings planted several years earlier.

In contrast to the above studies, growing evidence suggests that facilitation of trees by other vegetation is common in tropical forest successions. Chapman et al. (in press) found that tree survival was lower in vegetation-removal than in control plots 4 – 6 years after logging in a cypress plantation at Kibale. Fast-growing exotic tree species planted in degraded areas can initiate natural recruitment of native tree species (Lugo 1997; Parrotta et al. 1997; Otsamo 1998). And several studies provide strong evidence that shrub species can facilitate tree recruitment in abandoned pastures (Vieira et al. 1994; Aide et al. 1996; Da Silva et al. 1996; Zahawi & Augspurger 1999).

Predicting Interactions Among and Within Plant Communities

Assuming that positive and negative interactions exist between trees and other vegetation during succession, when should managers encourage facilitation by planting and/or retaining nurse plants or limit competition by removing vegetation? Facilitation of tree seedling recruitment and growth by taller vegetation may be most successful as a management strategy in harsh habitats (e.g. hot, cold, dry; Bertness & Callaway 1994; Callaway & Walker 1997; Holmgren et al. 1997). Interventions promoting facilitation may be most successful early in successions before a tall canopy develops and abiotic conditions improve. In some mild habitats, facilitation strategies may help to reduce competition with grasses and vulnerability to fire (Kuusipalo et al. 1995; Holl 1998b).

Predicting when and where plant competition will be important has been vigorously debated by plant ecologists (Grace 1991). One prominent argument

is that intensity of competition across ecosystems varies depending on environmental stress (Grime 1979). Another is that competition can be high in all ecosystems (Tilman 1985). In either case, competition can be expected to be less important early in succession when resources are abundant and/or plant biomass is low (Lambers et al. 1998). Furthermore because seedlings can temporarily rely on seed energy reserves and overall demands for resources are small relative to larger plants (Fenner & Kitajima 1999), competition is more likely between older stems than it is between seedlings (Callaway & Walker 1997). Thus, managers may expect to see a shift from facilitative to competitive interactions as successional forests develop, and vegetation thinning treatments may be helpful only later in succession when competitive interactions have intensified.

Our results and those of others suggest five guidelines for determining when and how to intervene to guide forest succession towards species-rich mature forest. First, species-level responses to intervention may be more important to consider than are community-level responses (e.g., growth form, successional guild). Thus, instead of conducting interventions over a uniform area, managers should target individuals of species whose growth responses to intervention are known (Guariguata 1999). This approach would also give managers a more active role in guiding forest composition to meet management goals (e.g., biodiversity conservation or timber production). Second, as described above, interventions to encourage facilitation should target seedlings, while interventions to limit competition should target older trees. One exception

may be small-seeded early-successional tree seedlings that require high light levels immediately after germination (Finegan 1984; Foster & Janson 1985; Fenner & Kitajima 1999). Third, to direct successions towards mature forest, managers should design treatments to prioritize late- over mid-successional species, and mid- over early-successional species. For example, early-successional trees could be thinned once high densities of mid-successional saplings have recruited. Fourth, since plant interactions during succession tend to be complex, managers should be cautious about assumptions concerning plant interactions. Finally, managers should monitor the success of interventions relative to control treatments, and be adaptable and creative with new strategies when interventions fail.

Currently, a great opportunity exists for advancing the field of tropical forest succession with more studies of plant interactions. In particular, we believe two types of studies are needed: experimental studies to separate complex interactions existing between species and broad-scale comparative studies to identify how plant interactions vary across ecosystems and disturbance types. Both approaches will be essential for advancing the ability of restoration ecologists to design successful management strategies.

Table 3-1. Initial and final medians (top number) and means (bottom number ± SD) for vegetation variables in control and shrub-removal plots. Initial shrub variables in removal plots after clearing were nil, and heights of stems < 1 m were not compared (both indicated by "-").

Stem variable	Stem height (m)			Density (stems/m^2)			Species richness (species/m^2)		
	Removal plot	Control plot	P value	Removal plot	Control plot	P value	Removal plot	Control plot	P value
Initial vegetation									
Tree	1.5	1.3	0.323	0.2	0.1	0.361	0.1	0.1	0.231
saplings	1.6 (0.8)	1.4 (1.0)		0.2 (0.1)	0.1 (0.1)		0.1 (0.1)	0.1 (0.1)	
Shrub	-	1.1	-	-	0.1	-	-	< 0.1	-
saplings		0.8 (0.7)			0.1 (0.1)			0.1 (0.1)	
Final vegetation									
Tree stems < 1 m tall	-	-	-	0	0.3	0.289	0	0.3	0.301
				0.2 (0.3)	0.2 (0.2)		0.4 (0.6)	0.2 (0.2)	
Shrub stems < 1 m tall	-	-	-	0.3	0.3	0.852	0.3	0.3	0.875
				0.2 (0.2)	0.4 (0.7)		0.3 (0.3)	0.2 (0.3)	
Tree	1.6	1.6	0.665	0.4	0.4	0.563	0.2	0.2	0.954
saplings	1.7 (0.4)	1.6 (0.5)		0.4 (0.2)	0.4 (0.2)		0.2 (0.1)	0.2 (0.1)	
Shrub	1.0	1.4	< 0.001	< 0.1	0.6	< 0.001	< 0.1	0.2	< 0.001
saplings	0.7 (0.7)	1.5 (0.6)		0.1 (0.1)	0.7 (0.6)		0.1 (<0.1)	0.2 (0.1)	

Table 3-2. Successional status (e = early-successional, m = mid-successional), numbers, and heights (m), of tree saplings in shrub-removal and control plots 16 mo after initial treatment. T-test results comparing sapling height and chi-square tests comparing sapling number between treatments are also presented (too few *F. africana* saplings were found for height comparisons).

Species	Successional status	Stem number			Stem height (m)		
		Removal plots	Control plots	P	Removal plots	Control plots	P
Albizia grandibracteata	e	29	19	0.195	1.6 (0.5)	1.6 (0.6)	0.971
Celtis africana	m	24	33	0.290	2.0 (0.7)	2.4 (0.9)	0.092
Celtis durandii	m	19	12	0.282	1.9 (0.5)	1.7 (0.9)	0.533
Diospyros abyssinica	m	38	36	0.888	1.4 (0.3)	1.5 (0.7)	0.243
Fagaropsis angolensis	m	3	8	0.227	1.6 (0.5)	1.4 (0.4)	-
Funtumia africana	m	19	14	0.488	1.9 (0.5)	1.7 (0.5)	0.361
Olea welwitschii	m	13	9	0.527	1.6 (0.5)	1.5 (0.3)	0.961
Trema orientalis	e	27	11	0.015	2.5 (1.0)	1.5 (0.5)	0.006

Table 3-3. Successional status (e = early-successional, m = mid-successional, l = late-successional), number, and mean (± SD) heights (m) of trees in vegetation-removal and control plots two years after initial treatment. P values from comparisons between treatments of sapling height (t-test) and stem number (chi-square) are also presented. Heights were not compared for species with < 6 stems per treatment, nor for stems < 1 m tall (both indicated by "-").

Species	Successional Status	Stem number			Stem height (m)		
		Removal plots	Control plots	P	Removal plots	Control plots	P
Cypress site, saplings ht ≥ 1 m							
A. grandibracteata	e	17	29	0.077	2.1 (2.4)	2.6 (1.3)	0.406
Bridelia micrantha	e	29	40	0.163	1.4 (0.4)	1.8 (0.6)	0.010
C. africana	m	9	12	0.603	1.9 (0.6)	1.6 (0.4)	0.202
C. durandii	m	5	18	< 0.001	1.3 (0.2)	1.7 (1.0)	-
Croton macrostachys	m	10	10	1.000	1.5 (0.3)	1.6 (0.4)	0.805
D. abyssinica	m	8	5	0.655	1.2 (0.2)	1.4 (0.3)	-
Maesa lanceolata	e	47	96	< 0.002	1.8 (0.8)	1.7 (0.6)	0.626
Milletia dura	e	8	3	0.252	1.7 (0.8)	6.0 (3.3)	-
T. orientalis	e	27	20	0.467	2.0 (1.3)	1.4 (0.6)	0.078
Cypress site, stems ht < 1 m							
A. grandibracteata	e	21	5	0.005	-	-	-
D. abyssinica	m	15	5	0.054	-	-	-
M. lanceolata	e	2	13	0.007	-	-	-
M. dura	e	9	3	0.166	-	-	-
T. orientalis	e	7	4	0.590	-	-	-
Pine site, saplings ht ≥ 1 m							
A. grandibracteata	e	37	54	0.538	2.5 (1.5)	2.5 (1.2)	0.814
C. africana	m	24	50	0.050	2.7 (1.4)	2.9 (1.3)	0.373
C. durandii	m	18	21	1.000	1.8 (1.2)	2.6 (1.9)	0.156
Clausena anisata	e	17	24	0.823	1.9 (0.8)	2.1 (0.9)	0.318
D. abyssinica	m	64	80	1.000	2.2 (0.8)	2.4 (0.9)	0.120
F. angolensis	m	5	9	0.708	3.4 (1.4)	2.9 (1.1)	-

Table 3-3 – continued.

Species	Successional Status	Stem number			Stem height (m)		
		Removal plots	Control plots	P	Removal plots	Control plots	P
Pine site, saplings ht ≥ 1 m							
F. africana	m	10	7	0.354	1.9 (0.5)	1.5 (0.5)	0.149
Maesopsis eminii	e	1	11	0.027	1.7	2.9 (1.3)	-
M. dura	e	10	25	0.083	3.4 (1.8)	3.8 (1.6)	0.549
Mimusops bagshawei	l	5	8	0.862	1.7 (0.8)	1.7 (0.8)	-
Polyscias fulva	e	8	12	0.862	2.3 (0.9)	2.8 (1.5)	0.430
Techlea nobilis	m	4	17	0.035	2.2 (0.4)	2.1 (1.0)	-
T. orientalis	e	251	185	< 0.001	4.5 (2.2)	5.8 (1.8)	< 0.001
Pine site, stems ht < 1 m							
A. grandibracteata	e	16	6	0.014	-	-	-
C. durandii	e	12	14	1.000	-	-	-
C. anisata	e	7	8	1.000	-	-	-
D. abyssinica	m	8	14	0.578	-	-	-

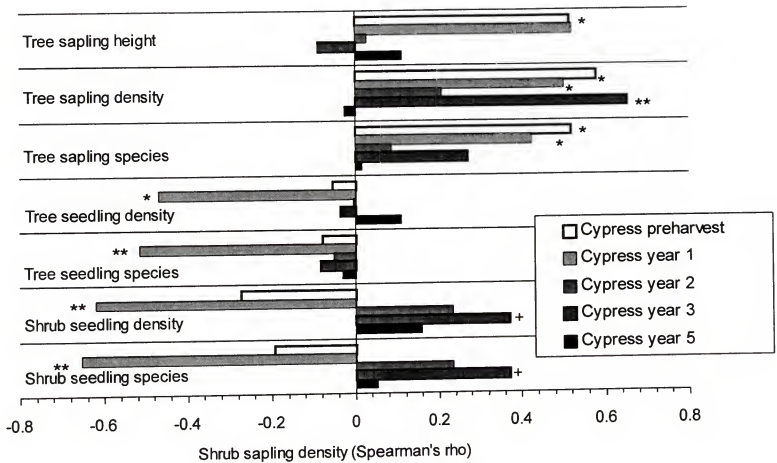

Figure 1. Results of Spearman rank correlations of shrub sapling density and tree sapling and tree and shrub seedling variables in unlogged and logged cypress plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

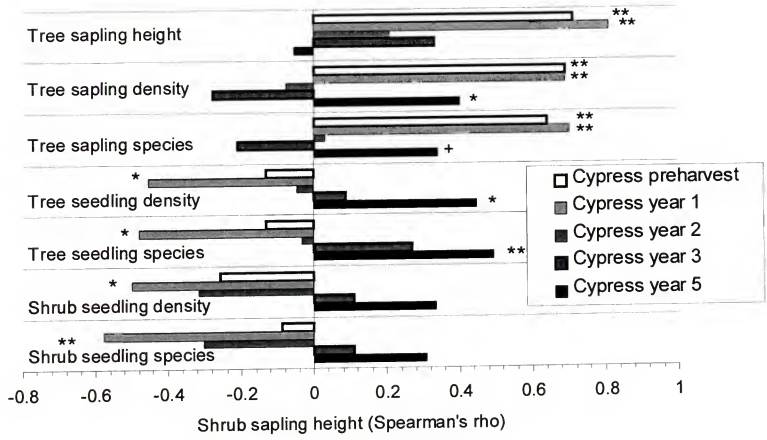

Figure 2. Results of Spearman rank correlations of shrub sapling height and tree sapling and tree and shrub seedling variables in unlogged and logged cypress plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

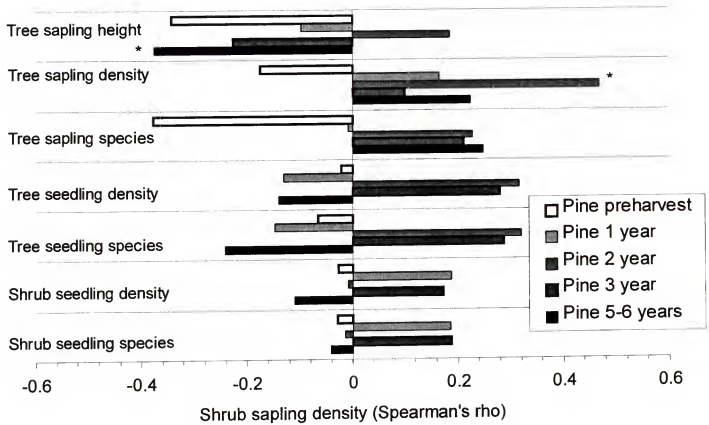

Figure 3. Results of Spearman rank correlations of shrub sapling density and tree sapling and tree and shrub seedling variables in unlogged and logged pine plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

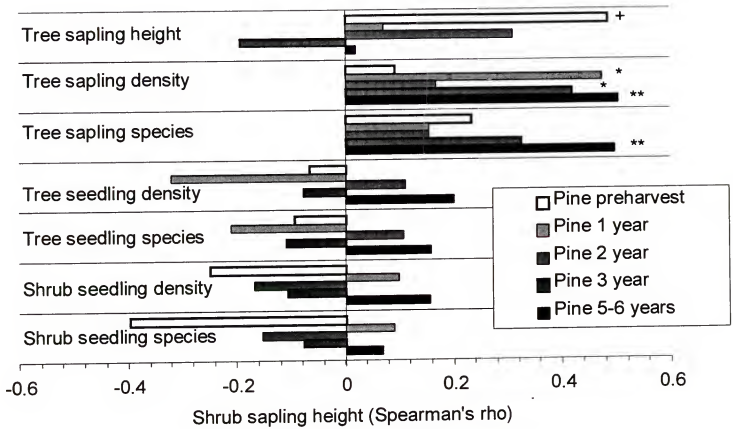

Figure 4. Results of Spearman rank correlations of shrub sapling height and tree sapling and tree and shrub seedling variables in unlogged and logged pine plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

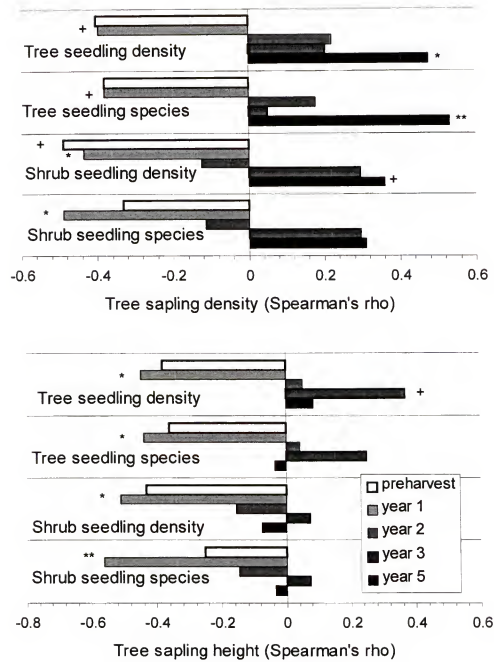

Figure 5. Results of Spearman rank correlations of tree sapling density and height with tree and shrub seedling variables in unlogged and logged cypress plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

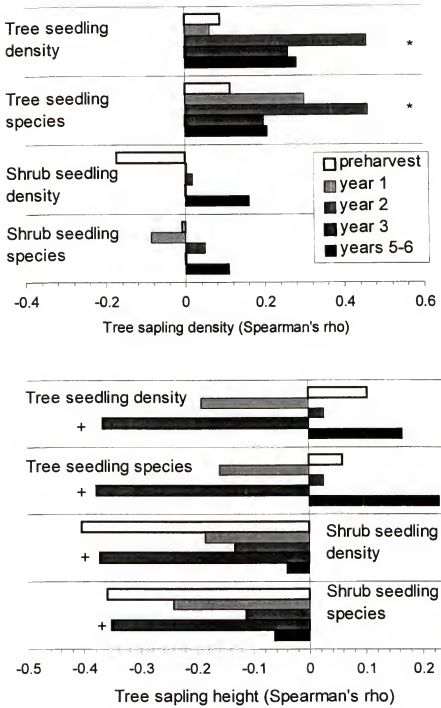

Figure 6. Results of Spearman rank correlations of tree sapling density and height with tree and shrub seedling variables in unlogged and logged pine plantations. * or ** indicate significance at $P < 0.05$ or $P < 0.01$, respectively; + indicate marginal insignificance at $P < 0.10$.

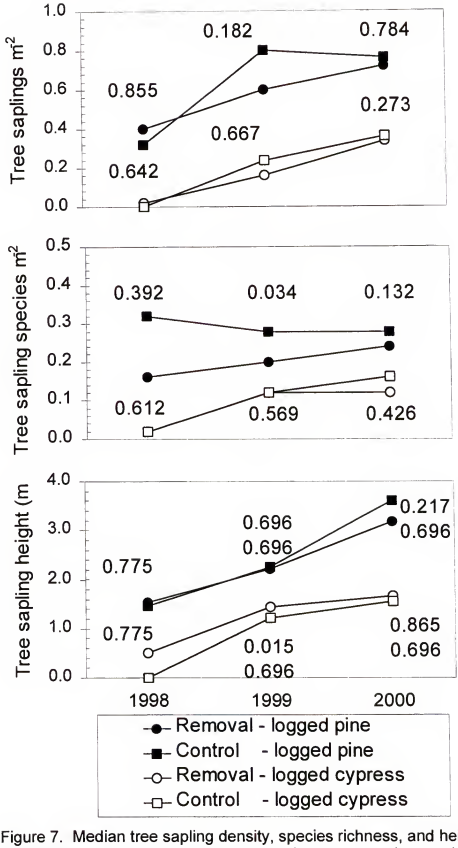

Figure 7. Median tree sapling density, species richness, and height during vegetation-removal experiments in early forest successions on logged pine and cypress plantations.

CHAPTER 4
EVALUATING STRATEGIES TO RESTORE FORESTS ON DEGRADED LANDS: TROPICAL FOREST SUCCESSION IN LOGGED SOFTWOOD PLANTATIONS IN UGANDA

Introduction

Forest regrowth is often slow or absent on heavily degraded lands in the tropics (Brown & Lugo 1990; Nepstad et al. 1996). Restored forests on these lands can be useful for biodiversity conservation, timber production, carbon-dioxide sequestration and other ecosystem services (Brown & Lugo 1990; 1994). Establishing exotic timber plantations on degraded lands can facilitate forest succession by providing an understory environment favorable for native plant recruitment (Chapman & Chapman 1996; Lugo 1997; Parrotta et al. 1997). An additional benefit to plantations as a restoration strategy is they may pay for themselves through sale of timber. While plantations have attracted the attention of tropical restoration ecologists, there has been little investigation of how best to use plantations in restoration (Ashton et al. 1998), how plantation harvest affects subsequent forest regrowth, or how using plantations compares to alternative restoration strategies. Furthermore, our understanding of general processes of forest succession is poor (Chazdon 1994), thus limiting our ability to manage secondary forests after plantation harvest.

In Kibale National Park, Uganda, we are studying forest regrowth after harvesting of exotic timber plantations. These plantations were planted for timber production in the 1950s and 1960s on previously forested, grass-dominated (especially *Pennisetum purpureum*) abandoned villages and croplands (Osmaston 1959; Sivell et al. 1996). Active fire exclusion was important to protecting young plantations, but became less necessary as plantations matured. As plantations matured, native tree and shrub species were allowed to establish in their understory (Chapman & Chapman 1996; Fimbel & Fimbel 1996). After logging, surviving native stems, the soil seed bank, and seed dispersal contribute to secondary forest growth. In contrast, similar areas that were not planted with exotics are still fire-maintained grassland, confirming that plantations can facilitate forest regrowth on degraded lands (Duncan & Duncan 2000; Zanne & Chapman in press).

Two successional trajectories emerge from logging of timber plantations at Kibale. As a result of differential recruitment of native stems prior to harvest (Fimbel & Fimbel 1996), logged pine plantations (*Pinus caribeae* and *P. patula*) have greater on-site initial recruit densities (e.g., more native stems) than do logged cypress (*Cupressus lusitanica*) plantations. The logged pine plantations are dominated by tree species, while the logged cypress plantations are dominated by both shrubs and trees. The juxtaposition of disturbed habitats with varying levels of initial recruit availability is common among degraded lands in the tropics (Uhl et al. 1982; 1988; Adedeji 1984; De Rouw 1994; Garciamontiel & Scatena 1994; Fernandes & Sanford 1995; Gillespie et al. 2000). Typically, more

heavily degraded sites start succession with lower recruit availability than do less degraded sites (Brown & Lugo 1990; 1994). Understanding how forest succession proceeds with different levels of initial recruit availability has not been well studied. However, such knowledge could be important for managers faced with choosing among disturbance types for investing restoration efforts. Or, this knowledge could be useful for managers predicting when successional forests will provide extractive resources or adequate habitat for species of interest.

We investigated four questions relevant to managing plantations for restoring forests and managing successional forests. First, how does initial recruit availability influence subsequent successional trajectories? To address this question, we compared the first six years of succession between logged cypress and pine plantations. Second, how does timber harvest affect ensuing forest succession? To address this question, we investigated how long a forest takes to regain the structure and composition present in the plantation understory before harvest, the damage inflicted on native stems during harvest, the effects of felling versus felling and removal of timber, and the effect of variation in disturbance intensity within and among logged plantations. Third, how easily can forest succession be enhanced through intervention? We examined whether experimental removal of all non-tree vegetation enhanced tree recruitment and growth, the success of planting tree and shrub seedlings into successional habitats of two ages, and leaving dead remnant trees in successional habitats to enhance seedling recruitment by attracting seed-dispersing birds. Fourth, how does using exotic timber plantations to restore forests compare with other

restoration strategies? Specifically, we contrasted forest succession among logged and unlogged plantations and a former grassland where fire was excluded since the time of plantation establishment. Finally, we evaluate pros and cons of using timber plantations to restore forests in light of our findings.

Methods

Study Site

Located on the foothills of the Ruwenzori mountains, Kibale National Park, Uganda, is dominated by moist-evergreen forest. Average elevation is 1500 m, and rainfall averages 1543 mm yr^{-1} (1903 - 1999), though it has increased to 1765 mm yr^{-1} in recent years (1991-1999). Softwood plantations in the park are surrounded by natural forest and have been described by Chapman and Chapman (1996), Fimbel and Fimbel (1996), and Zanne and Chapman (in press). Logging of plantations began in 1993 when Kibale became a national park, and current plans are to allow natural forests to grow back in their place. From 1998 – 2000 we studied forest succession among plantations logged between 1993 – 2000.

Mature cypress plantations have lower mean basal areas than do pine plantations (44.4 versus 71.3 m ha^{-1}, respectively), shorter canopies than do pine plantations (23 m versus 33 m, respectively), but similar mean DBHs relative to pine plantations (36 cm versus 36 cm, respectively;Fimbel & Fimbel 1996). Felling of timber is done with chainsaws, and many native trees and shrubs in the understory are crushed or damaged. Felled timber is rolled or winched to nearby

portable sawmills, pitsawing stations, or roadsides. During this movement, many more native stems are usually crushed or cut. When harvest is completed, few stems > 1 m tall remain. However, many seedlings survive logging, and root sprouts and coppice from native species are common.

Influence of Initial Recruit Availability

To assess the effect of initial recruit availability on succession, we quantified how vegetation differed between the only remaining unlogged cypress plantation and an adjacent unlogged pine plantation (thus controlling for site history and landscape position). Within each plantation, 15 plots were positioned by randomly choosing distances along a 100-m transect, then randomly choosing a distance of 1 - 60 m perpendicular to the transect. Plots were non-overlapping and within 100 m of natural forest edge. The openness of plantation understories allowed us to use 25-m^2 circular plots, which were faster to survey than were rectangular plots used in logged plantations. In these and all plots surveyed in logged plantations, we measured density, species richness, and height of shrub and tree stems $\geq$ 1.0 m tall. These stems were termed "saplings", though many shrub saplings were reproductively mature. Smaller (ht $\leq$ 0.25 m) and intermediate stems (ht = 0.26 – 0.99 m), were described in 4-m^2 circular subplots at the center of larger plots. We termed these smaller stems "seedlings," and intermediate stems as "large seedlings", though stems of both groups may have no longer been dependent on seed reserves or may have been sprouts. Plant identification was based on manuals by Eggeling and Dale (1952), Pohill (1952), Hamilton (1991), and Katende et al. (1995).

We compared vegetation in long-term plots in a pine and cypress plantation within a year after logging (~ 9 and ~ 4 months for the pine and cypress plantation, respectively). These were the only similarly-aged recently logged pine and cypress plantations available. Thirty plots (5 x 5 m) in each logged plantation were placed randomly (non-overlapping) along parallel transects (10 m apart) covering the entire logged area. All plots were within 100 m of natural forest edge. Plots were marked and surveyed again after two years; one plot in the logged pine plantation was destroyed by human activity before the second survey. During both surveys, vegetation was quantified as was done in unlogged plantations, though seedlings and large seedlings were sampled in 2 x 2 m corner subplots. Some sampled plots in the logged plantations were heavily disturbed areas (pit-sawing stations, portable sawmill locations, and roads) where soil and vegetation were more disturbed than in moderately disturbed plots where the main activity was felling and timber removal. Heavily disturbed plots were excluded from the present analyses, but are considered below. Many stems classified as seedlings in the first year after logging (44% and 23% of shrub and tree "seedlings", respectively) were actually root sprouts or coppice from stems buried during logging.

Finally, we surveyed the oldest successional habitats in logged plantations at Kibale (4 - 6 yrs after logging). Vegetation plots were surveyed in two cypress plantations, one logged 4 years before (n = 30 plots) and another logged 5 years before (n = 28 plots). Thirty plots were surveyed in a pine plantation logged 5 – 6 years before. In all these plantation, plot positioning and sampling followed that

of the long-term plots. We used 2 x 10 m plots in these areas to ease sampling of the dense vegetation; 2 x 2 m subplots for sampling smaller stems were placed at one end of the plot. Plots from the two logged cypress plantations were combined for comparison to plots in the logged pine plantation.

We used non-parametric analyses for these and most comparisons because our data were often highly zero-skewed. Consequently, we present medians to describe data, but we also provide means to aid comparisons with other studies where parametric analyses were used.

Harvesting Effects on Forest Succession

Native vegetation before and after timber harvest

From the surveys described above, we compared native vegetation present before logging to that at < 1 and 4 – 6 years after logging in moderately disturbed plots. Pine and cypress plantations were analyzed separately to control for differences in initial recruit availability.

Stem damage from logging

The process of felling and removing timber from plantations can severely damage aboveground native vegetation. When timber was cut, falling stems crushed many adjacent native stems, and most remaining native stems were cut to facilitate removal of logs. During sampling of plots in recently logged plantations, we classified surviving native stems into four categories: 1) undamaged, 2) bent – stems pinned to or near the ground by felled trees, 3) broken – stems broken near their base, and 4) cut – stems cut at their base.

Some stems fell in multiple damage categories. We pooled all plots (heavily and moderately disturbed, pine and cypress) and compared numbers of damaged stems to undamaged stems.

Damage from felling

When plantations are managed to promote natural forest regrowth, managers may want to develop harvest methods that reduce damage to native stems and encourage regeneration. Thus, it is important to know how damage during felling compares to that during timber removal. For reasons unknown to us, one section of pine plantation (0.4 ha) was felled and the timber left in place. This provided an opportunity to quantify damage to native stems from felling versus both felling and extraction. If damage from felling is relatively high, then techniques such as directional felling could be used to reduce native stem damage. Or, if damage from felling is high and sale of timber is not needed, plantation species could be girdled and left in place.

We sampled the area subjected only to felling in 1999, three years after timber had been cut (felled-only plots). Plot positioning and sampling followed that done in surveys of logged plantations. Plots (n = 20) were 2 x 10 m, with 2 x 2 m subplots for sampling stems < 1 m tall. We compared this successional habitat to the pine plantation logged 5 – 6 years previously (only moderately disturbed plots), the most similarly-aged logged pine plantation. Because another potential restoration strategy is leaving timber standing, we also compared felled-only plots to those in the unlogged pine plantation.

Within-site disturbance intensity

Damage inflicted on native stems during logging of plantations varies spatially, depending on intensity of harvest activity (e.g., portable sawmill locations vs. adjacent logged areas). We pooled plots from the two recently logged plantations (one pine and one cypress) and compared stem variables between plots on moderately (n = 49) and heavily disturbed (n = 10) sites.

We also compared effects on forest succession of two timber processing methods used in the same plantation. In one part of a pine plantation logged six years previously, felled timber had been winched or wheeled with a gurney to the roadside, then transported to a sawmill. In the other part of the plantation, each timber stem was felled, cut into logs, and manually rolled to a nearby pitsawing station (each station ~ 100 m^2). At pitsawing stations, logs were rolled onto scaffolding above a pit. Then, two men, one on the log and the other in the pit, used a large handsaw to cut the log lengthwise into boards. Where pitsawing was used to process timber, stations cover 20 – 30% of the area. Left at each station was a thick layer of sawdust, compacted soil, and timber scraps that potentially hindered forest regrowth more than in areas where stems were extracted for millsawing. In addition, the scaffolding was often constructed from native tree saplings cut from the plantation. On the other hand, while pitsawyers felled all timber, only the larger stems were processed, potentially leaving patches where native stems were less damaged than in areas where all stems were extracted for millsawing. We compared how these two timber processing methods affected forest regrowth by comparing vegetation plots that had been

randomly placed into either pitsawn or millsawn parts of the plantation (n = 16 and 10 plots, respectively).

Facilitating Forest Succession

Vegetation removal experiment

Resource competition among plants in early successional habitats could restrict the recruitment, growth, and survival of tree species (Holl 1998). To evaluate this, we removed all non-tree vegetation from 5 x 5 m randomly placed plots in the recently logged cypress plantation (~ 5 mo after logging; n = 22 plots) and pine plantation (~ 10 mo after logging; n = 20 plots). Approximately every four months (mean $\pm$ SD = 4.1 $\pm$ 1.5 mo), plots were cleared of all aboveground non-tree vegetation. Larger stems (height ~ > 0.5 m) were cut at the base, while smaller stems were pulled from the ground. Plots were surveyed when first cleared and two years later. During surveys, all tree saplings in the plots were identified, counted, and their heights measured; stems < 1 m tall were surveyed in 2 x 2 m a subplot placed at the center of each plot. Vegetation removal plots were compared to the vegetation plots of the same successional age in the same plantation (no heavily disturbed plots were included). Tree height, density, and species richness were compared between experimental and control plots for initial and final surveys. Seedling density and species richness were compared between treatments for final surveys.

Seedling planting experiment

Planting seedlings into successional habitats may be an effective way to overcome dispersal limitation and/or to improve the species composition or structure of developing forests (e.g. Tucker & Murphy 1997; Parrotta & Knowles 1999). We contrasted the success of nursery-raised seedlings transplanted into two plantations logged 7 – 20 months and 63 – 75 months earlier (hereafter "younger" and "older" site, respectively). Initially, the younger site was open with little vegetation above 0.25 m, but by the end of the experiment, it had a dense, short canopy (~ 1.5 m), composed of herbaceous growth, shrubs, and trees. Thus, general light quality shifted from direct to indirect sunlight during the experiment. The older site's canopy was 3.0 – 7.0 m tall, composed of tree saplings and shrubs; usually only indirect sunlight and sun flecks reached the understory.

Seedlings of local shrub and tree species were selected based on seed availability and nursery germination success. Seeds of each species were planted in nursery beds either in full sun or below a short (1 m) thatch roof. Planted seeds were watered every few days (unless it had rained) until seedlings were transplanted, usually 2 – 4 weeks after germination. Within a species, all transplanted seedlings had the same number of cotyledons and leaves, and were roughly the same height. After planting, seedlings were watered once (ca. 200 ml) to reduce mortality caused by transplanting. When possible, seedlings germinating in full sun were planted into the younger site (65% of the time), and seedlings germinating in shade were planted into the older site (94% of the time). When few seedlings germinated from one of the light treatments, seedlings were

taken from the other light treatment for both successional habitats (e.g., shade-germinated seedlings planted into the younger site). The length of time that transplanted seedlings were monitored varied among species because timing of germination varied. Altogether, 33 species were planted into the nursery, with 17 species producing enough seedlings for use in the experiment.

Seedlings were planted into the two successional habitats during the same or subsequent days. In the younger site, seedlings were planted along ten 50-m transects placed parallel to one another and separated by 10 m; seedlings stations were at 1-m intervals. Conspecifics were planted with 15-m minimum distance between them on transects. A similar design was used in the old successional habitat, but we used variable length parallel transects, each separated by a minimum of 5 m. We do not believe this difference in distance between parallel transects in the two treatments influenced seedling survivorship or growth for two reasons. First, there was a low probability that conspecifics on adjacent transects would be < 15 m apart (the minimum distance between conspecifics within a transect). And second, differences in planting densities between the treatment habitats were probably negligible relative to differences between treatment habitats for naturally occurring tree and shrub seedlings densities.

The proportion of seedlings surviving to the end of the experiment was calculated for each species, and the proportions from all species were compared between treatments. Within each species, proportions of surviving seedlings were also compared between treatments. For each seedling surviving to the end

of the experiment, relative growth rate (RGR) was calculated by subtracting the natural log of initial seedling height from the natural log of final seedling height, and dividing this difference by the number of days growth was monitored. In this experiment, RGR is a product of intrinsic and extrinsic (e.g., herbivory) factors. To look for overall differences in growth between treatments, a mean RGR was calculated for each species in each treatment, and means were compared between younger and older sites. Within each species, RGRs of individual seedlings were compared between treatments. Survival proportions and RGRs of early- versus mid- and late-successional species were also compared (the latter two categories were lumped due to low numbers of late-successional species). These designations were based on Eggeling (1952), Pohill (1952), Hamilton (1991), and Katende (1995) and our own observations.

Recruitment below snags

In one of the logged cypress plantations, many dead cypress trees remained standing (cause of death unknown). To determine whether these snags attracted seed dispersers and facilitated greater seedling recruitment than in adjacent areas without tall trees or snags, we surveyed seedlings below snags and in adjacent open areas at 17 – 19 months after logging. Twenty snags (ht $\geq$ 10 m) were randomly chosen from roughly 50 candidates, and a 2-m^2 plot was placed below the tallest part of each. A control plot was placed in a random direction 10 m from the snag in an area without snags or emergent trees. In both plots, all tree and shrub stems were identified, counted, and their heights measured.

Alternatives to Plantations – Fire Exclusion

Recurring fire is a severe impediment to forest succession on many degraded lands, especially grasslands (Uhl et al. 1988; Uhl & Kauffman 1990). One way plantations facilitate recruitment of native species on degraded lands is by reducing the flammability of habitats they replace and by encouraging fire prevention by managers (Kuusipalo et al. 1995). Thus, fire exclusion is one alternative to plantations as a restoration strategy.

Within one of the pine plantations is a section (1.7 ha) where pine seedlings were either not planted, or died soon after planting for unknown reasons (possibly drought or fire; B. Kisembo, Uganda Forestry Department, pers. comm.). It is thought that seedling death was not due to edaphic factors, since this plot was surrounded on three sides by mature pine plantations and on a fourth side by mature forest. This site and the adjacent pine plantations were fire-maintained grasslands when the pines were planted in the 1950s – 1960s. As the surrounding plantations matured, the maintenance of fire-breaks and reduction of grasses (probably due to shading) in plantation understories reduced or stopped the occurrence of fire to the site. After 40 – 50 years of fire-exclusion and forest regrowth, a well-developed successional forest now occupies the site. This forest represents a case study of forest succession following fire-exclusion on degraded grassland (hereafter "fire-excluded site").

The obvious control for assessing how effective fire-exclusion may be as a forest restoration tool are the Kibale grasslands that were never planted with timber species. While not resurveyed for this study, others have recently

documented that these areas are still fire-dominated grasslands where tree establishment and growth is minimal (Duncan & Duncan 2000; Zanne & Chapman in press). Given that fire-exclusion appears to promote forest succession, we wanted to compare it to the use of plantations as a forest restoration tool. Because establishing plantations and not harvesting them is one use of plantations as a restoration tool, we also compared successional forest in the fire-excluded site to that in the unlogged pine plantation. Because establishing plantations and later harvesting them is another use of plantations as a restoration tool, we compared successional forest in the fire-excluded site to that in the pine plantation surveyed 5 – 6 years after logging. Like many large-scale studies, the spatial replication of this design is limited. However, given that all three sites share a similar landscape position and site history prior to plantation establishment, this system provided a rare, large-scale opportunity to compare the use of fire-exclusion to plantations as a restoration strategy.

Twenty-five 20 x 2 m vegetation plots were placed in the fire-excluded site following the methods used in the unlogged and logged plantations. Vegetation sampling also followed the procedure used in the plantations. Small stems (ht < 1.0 m) were described in 2 x 2 m subplots.

Results

Influence of Initial Recruit Availability

Tree and shrub seedling density and species richness were similar between the unlogged pine and cypress plantation (Table 4-1), but the pine

plantation had significantly greater tree and shrub sapling density and species richness than did the cypress plantation. In the pine plantation, tree saplings were significantly taller, and there was a trend ("trend" = $0.05 < P \leq 0.10$ here and elsewhere) for taller shrub saplings than in the cypress plantation.

Within a year of logging, tree seedling density and species richness were similar between the pine and cypress plantations, but now significantly more shrub seedlings and seedling species were in the cypress (Table 4-1). The pine plantation still had significantly more tree saplings and sapling species, but shrub sapling density and species richness in the cypress now matched those in the pine plantation. Tree saplings were still significantly taller in the pine than in the cypress plantation, but shrub saplings were of similar heights in both plantations.

Four to six years after logging, tree seedling density and species richness were still similar between plantation types, but shrub seedlings were now significantly more dense and species-rich in the cypress than in the pine plantation (Table 4-1). Tree sapling density and species richness in the cypress plantation were now no different from those in the pine plantation. Shrub sapling density was now significantly greater in the cypress than in the pine plantation, but shrub species richness was still similar between plantation types. Tree and shrub sapling heights in cypress plantations were similar to those in the pine plantation.

Harvesting Effects on Forest Succession

Native vegetation before and after timber harvest

In the pine plantation, trees and shrubs were significantly or marginally more dense, species-rich, and taller before harvest than < 1 yr after harvest (Table 4-2). However, shrub seedling density was similar before and after logging, and tree seedlings were significantly more dense and species-rich after logging than they were before.

The pine plantation harvested 5 – 6 years previously had significantly more tree seedlings and tree seedling species than did the unlogged plantation (Table 4-2). Shrub seedling density and number of seedling species were similar between unlogged and logged plantations. Tree saplings were significantly more dense in the unlogged than in the logged plantation, though tree sapling species richness and height were similar between plantations. Shrub saplings were significantly taller, more dense, and more species-rich in the logged than in the unlogged plantation.

In cypress plantations, stem variables were generally similar before and within 1 yr of logging (Table 4-2). However, significantly more tree seedlings, shrub seedling species, shrub saplings, and marginally more sapling species were present after logging.

Cypress plantations logged 4 - 5 years before had significantly greater tree and shrub density, species richness, and heights than did the unlogged cypress plantation for both seedlings and saplings (Table 4-2). The one exception was that shrub seedling density was only marginally greater in logged than in unlogged plantation.

Stem damage from logging

During surveys, it was impossible to determine whether stems had survived logging or established after logging. Significantly more undamaged than damaged stems were found during surveys for all size classes (Table 4-3). Significantly more trees showed damage than did shrubs, probably because many of the shrubs were early-successional species established after logging. Saplings generally had significantly more damage than did smaller size classes, suggesting many smaller stems had recruited after logging. Nearly one-third of tree saplings found had been damaged during logging. One pioneer tree species, *Trema orientalis*, only established after logging, and when these stems were excluded, nearly half of all tree saplings showed damage from logging (Table 4-3).

Damage from felling

The felled-only site had significantly more tree seedlings, tree sapling species, and fewer shrub seedlings and shrub seedling species than in the unlogged pine plantation (Table 4-4). Tree saplings were significantly taller in the unlogged plantation than in the felled-only site, and there was a trend for more tree seedling species found in the felled-only than in the unlogged plantation.

Shrubs were significantly taller in the logged pine site (logged 5 – 6 years before) than in the felled-only site (Table 4-4). Among the other vegetation categories several trends for differences between these two sites were found, but no consistent pattern emerged.

Within-site disturbance intensity

Significantly more tree seedlings and tree seedling species were found in moderately disturbed than in heavily disturbed sites < 1 yr after logging (pine and cypress successional habitats pooled; Table 4-5). For all other stem variables, no differences existed between plot types.

When we compared regeneration between millsawn and pitsawn areas in the 6-year-old logged cypress plantation, significantly more shrub seedlings and seedling species (Mann-Whitney test, $P < 0.001$ and 0.003, respectively), and significantly more tree saplings and marginally more sapling species (Mann-Whitney test, $P = 0.014$ and 0.062, respectively) were found in millsawn than in pitsawn plots. Tree seedling and shrub sapling density and species richness were similar between the two areas (Mann-Whitney test, $P = 0.232$, 0.390, 0.771, and 0.153, respectively).

Facilitating Forest Succession

Vegetation removal experiment

Initial height, density, and species richness of tree saplings were similar between plots where all non-tree vegetation were removed and control plots in both the logged cypress and pine plantation (Mann-Whitney test, $P > 0.10$ for all contrasts; Table 4-6). After two years, height, density, and species richness of tree sapling and seedling variables in experimental plots were no different from those in control plots of either successional habitat (Table 4-6).

Seedling planting experiment

The average proportion of seedlings surviving to the end of the experiment was not significantly different between younger and older successional habitats (t-test paired by species, t = 0.8, P = 0.458, proportions were arcsine-square root transformed). Within either the older or younger successional habitat, there was no difference in proportion of seedlings surviving between early-successional versus mid- and late-successional species (Mann-Whitney test, P = 0.118 and 0.590, respectively; Table 4-7). When proportions surviving were compared within species, one late-successional species (*Uvariopsis congensis*) had significantly more stems surviving in the younger than in the older successional habitat (Table 4-7). Two early-successional species (*Maesopsis eminii* and *Polyscias fulva*) had significantly more seedlings surviving in the older successional habitat, and two others (*Securinega virosa* and *Trema orientalis*) had significantly more seedlings surviving in the younger successional habitat. Two other early-successional species (*Erythrococca trichogyne* and *Maesa lanceolata*) showed trends for greater survival in the younger successional habitat, while a third species (*Prunus africana*) showed a trend for greater survival in the older successional habitat. One late-successional species (*Monodora myristica*) showed a trend for greater survival in the older successional habitat.

With means from all species pooled, mean RGRs were similar between younger and older successional habitats (t-test paired by species, t = -1.0, P = 0.351). In both younger and older successional habitats, there was a trend for early-successional species to have greater RGRs than did mid- and late-

successional species (Mann Whitney test, P = 0.079 and 0.064, respectively). RGRs within species differed significantly between the two successional habitats for several species (Table 4-7). For three early-successional species (*Erythrina excelsa*, *Prunus africana*, and *Erythrococca trichogyne*), RGRs for seedlings in the younger successional habitat were significantly greater than were those in the older successional habitat. For a fourth early-successional species (*Polyscias fulva*) and one late-successional species (*Monodora myristica*), RGRs were significantly greater in the older successional habitat. Four species showed trends or significant differences between treatments for both RGR and survival. Oddly, two of these had better growth but lower survival in the sun (*P. africana* and *P. fulva*).

Recruitment below snags

Density and species richness of animal-dispersed tree seedlings and shrub saplings were significantly greater below snags than control plots (Table 4-8). However, animal-dispersed shrub seedling and tree sapling density and species richness were similar between snag and control plots. All categories of non-animal-dispersed stems were similar between snag and control plots (Mann-Whitney tests, P > 0.10 for all contrasts) suggesting these areas were similar for other factors potentially affecting recruitment.

Alternatives to Plantations – Fire Exclusion

The successional forest on the fire-excluded site had a tall (15 – 25 m), closed canopy of *Albizia grandibracteata* trees, with an open understory

composed mainly of tree saplings and few shrubs. This site had significantly greater values for most tree variables than did the unlogged pine plantation (Table 4-9). In contrast, shrub variables were generally similar between the unlogged pine plantation and the fire-excluded site. When the fire-excluded site was compared with the logged pine plantation after 5 – 6 years of regrowth, the former had significantly more tree seedlings and taller tree saplings, but had fewer tree saplings and sapling species. Shrub seedling variables were similar between the logged pine and fire-excluded site, but shrub sapling variables were significantly greater in the logged pine.

Discussion

Our results provide insight into how exotic tree plantations can initiate forest regrowth in arrested successional habitats, a restoration strategy that has recently received much interest from researchers and managers. Below, we relate our findings to four considerations for using plantations as a restoration tool: the influence of initial recruit availability; harvesting effects on succession; ways to encourage succession; and, alternatives to using plantations.

Influence of Initial Recruit Availability

Differences in tree and shrub stem variables in the unlogged pine and cypress plantations led to differences in postharvest succession between plantation types. Fimbel and Fimbel (1996) found similar patterns between unlogged pine and cypress plantations in Kibale and hypothesized these

differences arose from faster maturation rates of pines than the cypress, more understory light in the pine than in the cypress, and greater seed dispersal into pine than into cypress plantations. Differences between plantations do not appear to have resulted from soil or landscape position differences between plantation types (Osmaston 1959; Fimbel & Fimbel 1996). Studies elsewhere in the tropics have also found differences in native stem recruitment among plantation types (Parrotta 1995; though see Geldenhuys 1997; Keenan et al. 1997; Powers et al. 1997; Parrotta 1999; Otsamo 2000), suggesting post-harvest forest succession will vary among plantations in other regions.

Because of differences in native stem variables between the unlogged pine and cypress, we expected forest regrowth in logged cypress plantations to be slower than in logged pine plantations. While true during the first few years of succession, by 4 – 6 years tree sapling density and species richness were similar between the successional habitats. This may have partially resulted from seed dispersal by birds attracted to early-successional fruiting shrubs in logged cypress plantations. This rapid convergence suggests that managers may not always want to invest resources into accelerating succession on sites with low initial recruit densities. For example, if managers at Kibale want successional forest structure in recently logged cypress plantations to match that in recently logged pine plantations, they could intervene in the logged cypress plantations (e.g., seedling planting), or wait 5 – 10 years for unassisted convergence with succession in the logged pine plantations. When management goals are more specific (e.g., obtaining a certain density for one species), waiting for

convergence may not be sufficient. The difficulty will be predicting when convergence will happen naturally, or when intervention is needed.

Other studies of succession in the tropics have not found much evidence for convergence. In Nigeria, Adedeji (1984) found no convergence in stem recruitment after two years of succession where slash was either burned or removed after forest clearance. Uhl et al. (1982; 1988a) found no convergence during the first 3 – 8 years of succession following light, moderate, or heavy pasture use in Amazonia. In Puerto Rico, Aide et al. (1996) found that secondary forest structure resembled undisturbed forest after 40 years of succession. Rates of convergence among successional habitats probably depend on various factors, including the severity of site degradation and availability of seed sources and seed dispersers. Managers should be cautious about assuming whether convergence will occur among different types of successional habitats.

Harvesting Effects on Forest Succession

Logging in the cypress plantations appeared to significantly reduce the quantities of some stem variables, and increase the quantities of stem variables. In contrast, logging in the pine plantation led to declines within a year for most stem variables, although these declines did not persist. This difference in loss of native stems during logging probably resulted from unlogged pine plantations having twice the density of timber stems than did unlogged cypress plantations (Fimbel & Fimbel 1996). Thus, there was probably greater damage to native stems during harvest in pine than in cypress plantations.

Our results suggest that forest succession is slower in unlogged plantations than in logged plantations. While we have no information about native stem recruitment rates in unlogged plantations, secondary forests in the older successional habitats appear to be much better developed than do those in unlogged plantations. Similarly, Otsamo (1998) found that removal of plantation species enhanced seedling growth of a forest dipterocarp species on degraded grassland. Ashton (1998) found that removal of pine overstory enhanced growth of some late-successional tree species that had been planted within plantations.

We need to know when to harvest during plantation maturity to maximize native tree recruitment. Because native stems become bigger and, initially, more dense as plantations age (Geldenhuys 1997; Keenan et al. 1997; Parrotta 1999), harvesting when plantations are older may be better. On the other hand, if logging techniques will be very destructive to the native plant community, then logging when the plantation is young may avoid massive loss of above-ground native stem biomass.

While logging seemed to promote forest succession, the harvesting process killed many native trees and left many surviving stems heavily damaged. Our data provide weak support that leaving felled timber in place is better for tree growth and recruitment and shrub suppression than is extracting felled timber or not felling timber at all. However, because leaving felled timber on-site forfeits profits from timber sales, it not be a popular restoration strategy, anyway. Instead, managers could plan timber extraction protocols that limit damage to native stems during harvest. For example, timber stems could be directionally

felled to avoid dense patches of native vegetation or native species of particular interest. Because much damage to native stems occurs when timber is extracted, in some areas timber could be felled but not extracted. Any extraction techniques reducing damage to native stems will also benefit succession. For example, in one small plantation at Kibale that was not studied, timber was removed by pulling stems out with a cable and motorized winch, thus sparing many native trees.

Variation in harvesting activities within logged forests can produce spatial variation in forest regrowth (Pinard et al. 2000); however in our study the intensity of disturbance affected only some stem categories. Shrub stems were similar between moderately and heavily disturbed sites, as might be expected given their fast recruitment and growth rates. However, fewer tree seedlings were found in heavily than in moderately disturbed plots, suggesting tree seedling recruitment is more sensitive to disturbance than is shrub seedling recruitment; tree saplings were similar in both disturbance types, perhaps due to their overall low densities early in succession. When we compared millsawn and pitsawn areas within a single plantation, we found greater tree sapling and shrub seedling densities in the millsawn than in pitsawn plots, but shrub sapling and tree seedling densities were similar between treatments. Together, these results suggest the impact of disturbance intensity on recruitment, will vary between trees and shrubs, and seedlings and saplings.

Facilitating Forest Succession

We quantified whether vegetation removal, direct plantings, and leaving snags helped facilitate forest succession in logged plantations. These interventions were within early successional habitats, a time when succession is potentially more tractable than it is later when it becomes more difficult to alter composition or structure of vegetation.

Previous studies have indicated that vegetation removal can have either positive or negative effects on forest succession. Successional habitats often have high densities of non-tree vegetation that may limit tree recruitment and growth (Tilman 1990; Putz & Canham 1992; Berkowitz et al. 1995; Sun & Dickinson 1996; Holl 1998). On the other hand, harsh abiotic conditions of recently disturbed habitats can be unfavorable for tree establishment (Aide & Cavelier 1994; Brown & Lugo 1994), and the shade provided by non-tree vegetation may help trees establish and grow (Nepstad et al. 1991; Vieira et al. 1994; Zahawi & Augspurger 1999). Our experimental removal of all non-tree vegetation produced no net positive or negative effect on recruitment, survival, or growth of trees at the community level. This suggests that any facilitative and inhibitive effects of non-tree vegetation on trees were weak, or that they offset each other. We conclude that removal of non-tree vegetation at our site does not seem to be a beneficial management strategy in early-successional habitats, although it may be useful for particular tree species. Chapman et al. (in press) found that tree density declined in plots in which vegetation was removed in a 4 – 6-year-old successional habitat on logged cypress plantation at Kibale. In contrast, others have found that thinning of non-tree vegetation in successional

habitats enhances tree recruitment and growth (Holl 1998; Otsamo 1998; Guariguata 1999). Until more is known, managers should be cautious about assuming that removing non-tree vegetation will benefit forest regrowth in early successional habitats.

Less than half of seedlings we planted into successional habitats at Kibale survived, and age of successional habitat was important only for a few species. Direct seedling planting into degraded habitats tends to be a successful strategy, although it is expensive, time consuming, and labor intensive (Tucker & Murphy 1997; Parrotta & Knowles 1999). Direct planting overcomes recruitment limitations due to limited seed dispersal, high seed predation, and poor germination. However, seedlings are vulnerable to other hazards in disturbed habitats including herbivory, water-stress, and shading from adjacent plants. The limited success seen in our study, and probably elsewhere, could be improved if plantings of individual species were timed to optimize survival and growth.

We found greater density of animal-dispersed tree seedlings and shrub saplings below snags than in adjacent areas without snags. However, animal-dispersed tree saplings and shrub seedlings were similar between snag and control plots. One explanation for this pattern is that optimal conditions for recruitment were early during succession for shrub species and later for tree species. Non-animal-dispersed species were similar between snag and control plots suggesting that above patterns were not due to differential recruitment conditions. Seed rain is usually greater below emergent perches than in adjacent open areas of other disturbed tropical systems (Holl 1998; Duncan &

Chapman 1999; Toh et al. 1999). Dispersal to emergent perches may be especially important where other vegetative resources for succession are absent. However, enhanced seed dispersal must be coupled with favorable conditions for seedling recruitment (Holl 1998), and the effectiveness of snags or other perches may be limited since they often cover only small portions of degraded areas.

Alternatives to Plantations – Fire Exclusion

We contrasted forest succession in the fire-excluded site to two possible plantation strategies: leaving or extracting plantation trees. We found that tree recruitment and growth were better in the fire-excluded site than in the unlogged pine plantation. When we compared the fire-excluded site and the logged pine plantation, tree sapling density in the fire-excluded site was twice that in the logged plantation. Other stem variables were similar between treatments or greater in the logged plantation. Emphasizing tree sapling recruitment, these results suggest that fire exclusion is a better strategy than is establishing plantations and either harvesting or leaving the timber. Fire-exclusion will be an inexpensive strategy relative to other interventions and can be used over large areas. However, successional habitats will need constant protection from fire until they become less flammable, and fire exclusion will not provide the financial benefits possible through timber production.

Plantations as a Restoration Tool

If plantations are used as a restoration strategy, then we need to know more about how to use them to maximize native tree recruitment and growth.

Our findings suggest that felling and extracting exotic stems benefit forest succession more than does leaving timber intact. Girdling timber and leaving stems standing, or felling timber and leaving fallen stems in place may enhance succession similar to felling and extraction. These latter strategies may be appropriate for benefiting a native stem understory when selling timber is not a priority and/or when there is no market for harvested timber. However, fire exclusion seems to be just as or more effective than are any of these plantation-oriented restoration strategies.

Approaches using a combination of strategies may be particularly useful (Lamb 1998). For example, large degraded grasslands could be protected by fire breaks. Smaller areas within the grassland could be planted with timber species to generate income, an extractable resource, and an alternative restoration strategy if fire exclusion fails.

Unfortunately, any restoration program using plantations to enhance native stem colonization and generate salable timber faces a conflict of interest. Allowing an understory of native species to develop will slow timber growth. Thus, there is temptation to manage plantations for profit rather than for conservation priorities (Lamb 1998). Furthermore, managers may decide to replant harvested plantations with more timber species rather than allowing natural forest succession to proceed. For these reasons, managers and institutions backing them need to consider the non-monetary values of restoring biodiversity, (Lamb 1998).

Non-ecological challenges to using plantations as a restoration strategy exist (Lamb 1998). Predicting profits from the sale of timber involves estimating the market value of timber several decades in advance. This may be difficult since market prices depend on fluctuating local, regional, and global timber supplies (Leslie 1999). In addition, there can be a constant temptation to manage plantations for profit rather than for conservation priorities (Lamb 1998). For example, managers may decide to replant harvested plantations with more timber species rather than allowing natural forest succession to proceed.

Table 4-1. Median (top number) and mean (bottom number ± SD) density (stems/m^2), species richness (species/m^2), and height (m) for trees and shrubs in unlogged and logged pine and cypress plantations. Results of Mann-Whitney contrasts between the plantation types within a successional age are also presented: *** = P ≤ 0.001, ** = P ≤ 0.01, * = P ≤ 0.05, $^+$ = P ≤ 0.10.

Stem Variable	Unlogged			6 months			4 – 6 years		
	Pine	P	Cypress	Pine	P	Cypress	Pine	P	Cypress
Tree seedling density	0.25		0.25	0.75		0.75	1.50		1.00
	0.38 (0.45)		0.32 (0.36)	1.33 (1.31)		1.70 (2.80)	2.43 (3.47)		2.41 (3.08)
Tree seedling species richness	0.25		0.25	0.50		0.50	0.50		0.50
	0.28 (0.28)		0.27 (0.27)	0.60 (0.55)		0.54 (0.51)	0.60 (0.50)		0.56 (0.38)
Shrub seedling density	0.25		0.50	0	**	0.75	0.13	**	0.50
	0.42 (0.58)		0.60 (0.92)	0.31 (0.56)		2.52 (4.85)	0.51 (0.79)		0.97 (1.15)
Shrub seedling species richness	0.25		0.25	0	***	0.50	0.13	**	0.50
	0.25 (0.21)		0.22 (0.23)	0.12 (0.19)		0.59 (0.58)	0.27 (0.34)		0.48 (0.36)
Tree sapling density	0.64	***	0.04	0.32	***	0.02	0.48		0.50
	0.79 (0.38)		0.11 (0.19)	0.49 (0.44)		0.09 (0.18)	0.59 (0.42)		0.67 (0.58)
Tree sapling species richness	0.28	***	0.04	0.16	***	0.02	0.25		0.30
	0.26 (0.05)		0.07 (0.08)	0.18 (0.10)		0.05 (0.07)	0.25 (0.14)		0.30 (0.18)
Shrub sapling density	0.36	***	0.08	0.24		0.36	0.60	***	0.90
	0.39 (0.26)		0.09 (0.08)	0.27 (0.24)		0.46 (0.52)	0.62 (0.34)		0.98 (0.46)
Shrub sapling species richness	0.16	***	0.04	0.08		0.12	0.23		0.25
	0.15 (0.07)		0.06 (0.05)	0.10 (0.06)		0.10 (0.08)	0.22 (0.10)		0.25 (0.07)
Tree sapling height	2.90	***	1.12	1.46	***	0	5.47		4.98
	2.91 (0.42)		1.30 (1.47)	1.67 (0.59)		0.74 (1.09)	6.08 (3.25)		5.64 (4.01)
Shrub sapling height	2.08	+	1.29	1.37		1.28	5.63		5.66
	2.58 (0.97)		2.07 (2.64)	1.24 (0.54)		1.09 (0.68)	5.20 (1.77)		5.59 (1.32)

Table 4-2. Results (P values) of Mann-Whitney comparisons of stem density (stems/m^2), species richness (species/m^2), and height (m) between unlogged (UL) and logged (L) plantations. Where differences were detected, directions of results are indicated (see Table 4-1 for stem variable values).

Stem Variable	Unlogged vs. 6 mo. after logging		Unlogged vs. 4-6 yr. after logging	
	Pine	Cypress	Pine	Cypress
Tree seedling density	0.014 L > UL	0.042 L > UL	0.007 L > UL	< 0.001 L > UL
Tree seedling species richness	0.051 L > UL	0.112	0.041 L > UL	0.008 L > UL
Shrub seedling density	0.154	0.152	0.980	0.060 L > UL
Shrub seedling species richness	0.038 UL > L	0.051 L > UL	0.701	0.003 L > UL
Tree sapling density	0.010 UL > L	0.689	0.047 UL > L	< 0.001 L > UL
Tree sapling species richness	< 0.001 UL > L	0.450	0.744	< 0.001 L > UL
Shrub sapling density	0.087 UL > L	0.012 L > UL	0.023 L > UL	< 0.001 L > UL
Shrub sapling species richness	0.023 UL > L	0.066 L > UL	0.018 L > UL	< 0.001 L > UL
Tree sapling height	< 0.001 UL > L	0.390	0.001 L > UL	< 0.001 L > UL
Shrub sapling height	< 0.001 UL > L	0.748	< 0.001 L > UL	< 0.001 L > UL

Table 4-3. Percentages of surviving native stems with and without damage within one year of logging and extraction of timber species. Three damage categories, total percent damaged, percent undamaged stems, and total stem number are presented. Also presented are results of Wilcoxon signed rank tests comparing for each stem category the total damaged and undamaged stems in plots. For trees, percentages of undamaged stems when *T. orientalis* is excluded are presented in parentheses.

Growth form	Stem size class	Bent	Broken	Cut	% Total damaged stems	% Undamaged stems	Total stems	P
Shrub	Seedling	0.6	1.9	0.3	3.2	96.8	316	< 0.001
	Large seedling	2.1	2.4	0.0	4.8	95.2	289	< 0.001
	Sapling	3.5	1.3	0.2	5.3	94.7	541	< 0.001
Tree	Seedling	3.2	3.5	0.3	7.0	93.0 (87.1)	345	< 0.001
	Large seedling	3.7	12.0	3.3	19.8	80.2 (74.6)	242	< 0.001
	Sapling	11.7	7.3	11.3	32.3	67.7 (57.6)	452	0.002

Table 4-4. Medians (top number) and means (bottom number ± SD) for tree and shrub density (stems/m^2), species richness (species/m^2), and height (m) from felled-only plots. Felled-only plots (F) were compared to unlogged (U) and pine plantations logged 5 – 6 years previously (L). Directions of significant or marginally insignificant differences are indicated below P values (Mann-Whitney tests; see Table 4-1 for stem variables for unlogged and logged plantations).

Stem Variable	Median and mean (SD) Felled-only	Felled-only vs. Unlogged	Felled-only vs. Logged
Tree seedling density	1.13 1.76 (2.57)	0.002 F > U	0.669
Tree seedling species richness	0.50 0.45 (0.24)	0.064 F > U	0.362
Shrub seedling density	0 0.11 (0.17)	0.043 U > F	0.052 L > F
Shrub seedling species richness	0 0.10 (0.15)	0.046 U > F	0.101 L > F
Tree sapling density	0.73 0.74 (0.33)	0.856	0.081 F > L
Tree sapling species richness	0.33 0.33 (0.10)	0.025 F > U	0.054 F > L
Shrub sapling density	0.38 0.50 (0.38)	0.633	0.066 L > F
Shrub sapling species richness	0.20 0.19 (0.07)	0.214	0.218
Tree sapling height	3.84 4.27 (1.39)	0.001 U > F	0.068 L > F
Shrub sapling height	2.84 2.98 (0.82)	0.182	< 0.001 L > F

Table 4-5. Medians (top number), means (bottom number ± SD), and Mann-Whitney comparisons of stem density (stems/m^2), species richness (species/m^2), and height (m) from plots in heavily and moderately disturbed sites in pine and cypress plantations sampled < 1 yr after logging.

Stem Variable	Intensely disturbed plots	Moderately disturbed plots	P value
Tree seedling density	0 0.93 (2.25)	0.75 1.51 (2.16)	0.042
Tree seedling species richness	0 0.25 (0.41)	0.50 0.57 (0.53)	0.037
Shrub seedling density	0.50 1.03 (1.26)	0.25 1.39 (3.56)	0.647
Shrub seedling species richness	0.25 0.38 (0.40)	0.25 0.35 (0.49)	0.645
Tree sapling density	0.18 0.22 (0.21)	0.20 0.29 (0.39)	0.984
Tree sapling species richness	0.08 0.09 (0.06)	0.08 0.11 (.011)	0.652
Shrub sapling density	0.20 0.38 (0.49)	0.24 0.36 (0.41)	0.626
Shrub sapling species richness	0.08 0.10 (0.11)	0.12 0.10 (0.07)	0.806
Tree sapling height	1.42 1.57 (1.23)	1.30 1.27 (0.97)	0.489
Shrub sapling height	1.32 1.03 (0.93)	1.30 1.18 (0.60)	1.000

Table 4-6. Median (top number) and mean (bottom number ± SD) height (m), density (stems/m^2), and species richness (species/m^2) for trees in plots cleared of all non-tree vegetation versus unmanipulated controls. Treatments were compared with Mann-Whitney tests, but no differences ($P > 0.10$ for all contrasts) were found.

Plantation and year	Tree size class	Height		Density		Species Richness	
		Control	Cleared	Control	Cleared	Control	Cleared
Logged cypress plantation							
Year 1	Saplings	0 0.74 (1.09)	0.5 0.83 (1.25)	0.02 0.09 (0.18)	0.02 0.06 (0.09)	0.02 0.05 (0.07)	0.02 0.05 (0.07)
Year 3	Seedlings	-	-	0 0.15 (0.20)	0 0.20 (0.53)	0 0.14 (0.17)	0 0.09 (0.20)
	Saplings	1.56 1.70 (1.11)	1.68 1.62 (1.03)	0.36 0.52 (0.46)	0.28 0.35 (0.29)	0.16 0.18 (0.12)	0.12 0.16 (0.12)
Logged pine plantation							
Year 1	Saplings	1.46 1.67 (0.59)	1.53 1.52 (0.37)	0.32 0.49 (0.44)	0.4 0.75 (1.21)	0.16 0.18 (0.10)	0.16 0.16 (0.07)
Year 3	Seedlings	-	-	0 0.23 (0.36)	0.13 0.40 (0.71)	0 0.17 (0.25)	0.13 0.24 (0.30)
	Saplings	3.60 3.72 (1.15)	3.16 3.28 (1.15)	0.76 0.89 (0.59)	0.72 0.95 (0.96)	0.28 0.30 (0.12)	0.24 0.24 (0.09)

Table 4-7 Relative growth rates (RGR; change in height/day) and proportions surviving for seedlings transplanted into younger and older successional habitats (averaging 14 and 69 months after logging, respectively). Provided for each species is successional guild ("status"; E = early-, M = mid-, and L = late-successional), sample number, number of days seedlings were monitored, and mean initial height. P values for RGR and proportion surviving are from Mann-Whitney tests and chi-square tests, respectively. * = species that germinated only from sun plots.

Seedling species	Guild	Number planted		Days observed	Mean height	RGR per 100 days			Proportion surviving		
		young	old		(cm)	young	old	P value	young	old	P value
Trees											
Albizia grandibracteata	E	30	30	171	3.9	0.34	0.29	0.325	0.37	0.47	0.549
Aphania senegalensis	L	30	30	132	6.8	-0.01	0.09	0.325	0.60	0.70	0.631
Bridelia micrantha	E	15	12	358	4.1	0.41	0.40	0.624	0.27	0.25	0.933
Celtis durandii	M	30	23[Ψ]	374	3.6	0.37	0.27	0.302	0.20	0.30	0.440
Cordia abyssinica	M	30	30	41	3.0	1.53	1.18	0.588	0.20	0.37	0.225
*Diospyros abyssinica**	M	15	15	359	5.3	0.07	0.06	0.837	0.60	0.67	0.819
Erythrina excelsa	E	30	30	172	5.8	1.13	0.68	< 0.001	0.67	0.70	0.876
*Fagaropsis angolensis**	M	9	8	179	2.5	0.54	0.42	1.000	0.22	0.38	0.560
*Maesa lanceolata**	E	30	30	443	0.5	0.87	0.83	0.617	0.20	0.03	0.059
Maesopsis eminii	E	30	30	384	6.1	0.24	0.35	0.384	0.03	0.30	0.011
*Monodora myristica**	L	30	30	309	11.0	-0.37	0.02	<0.001	0.33	0.77	0.024
Polyscias fulva	E	30	30	384	3.0	0.58	0.37	0.021	0.10	0.50	0.005
*Prunus africana**	E	30	15	440	5.3	0.46	0.31	0.002	0.63	0.67	0.095
Trema orientalis	E	30	30	440	1.3	0.40	-	-	0.27	0.00	-
*Uvariopsis congensis**	L	30	15	261	7.3	-0.04	0.07	0.230	0.13	0.53	0.006
Shrubs											
*Erythrococca trichogyne**	E	30	30	447	1.7	0.60	0.43	0.005	0.73	0.40	0.086
Securinega virosa	E	30	30	434	0.8	0.64	0.82	0.752	0.33	0.03	0.007
Mean (all species)				313	4.2	0.46	0.41		0.35	0.42	
SD (all species)				129	2.7	0.46	0.32		0.22	0.25	

[Ψ] 18 of these seedlings germinated in shade plots.

Table 4-8. Median (top number) and mean (bottom number ± SD) density (stems/m^2) and species richness (species/m^2) of seedlings and saplings below snags and in adjacent control areas within a cypress plantation 1.5 years after logging. Results of Wilcoxon Signed Rank comparisons are presented: *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$, $^{+}$ = $P \leq 0.10$.

Stem variable	Density			Species richness		
	Snag plots	P	Control plots	Snag plots	P	Control plots
Tree seedlings	0.75 1.83 (2.40)	*	0.25 0.40 (0.50)	0.5 0.80 (0.89)	*	0.25 0.33 (0.37)
Shrub seedlings	0 0.13 (0.28)		0 0.18 (0.34)	0 0.10 (0.21)		0 0.15 (0.29)
Tree saplings	0 0.73 (1.07)		0.50 0.53 (0.47)	0 0.48 (0.60)		0.50 0.48 (0.41)
Shrub saplings	1.50 1.30 (0.89)	*	0.50 0.83 (0.83)	0.50 0.70 (0.44)	*	0.50 0.48 (0.38)

Table 4-9. Median and mean native stem density (stems/m^2), species richness (species/m^2), and height (m) from the fire-excluded site, and results of Mann-Whitney contrasts (P values) between this site and logged and unlogged pine and cypress plantations. The direction of significant differences is indicated below P values. Marginally insignificant trends are indicated within parentheses (see Table 4-1 for stem variables for unlogged and logged plantations).

Stem variable		Contrasts with fire-excluded site (FES)	
	Median and mean (SD)	Unlogged pine (UP)	Logged pine (LP)
Tree seedling density	0.50 0.93 (0.91)	0.031 FES > UP	0.104 LP > FES
Tree seedling species richness	0.50 0.47 (0.34)	0.079 FES > UP	0.383
Shrub seedling density	0.50 0.48 (0.42)	0.322	0.386
Shrub seedling species richness	0.25 0.27 (0.24)	1.000	0.481
Tree sapling density	1.00 0.90 (0.38)	0.240	0.003 FES > LP
Tree sapling species richness	0.35 0.35 (0.15)	0.021 FES > UP	0.028 FES > LP
Shrub sapling density	0.20 0.24 (0.19)	0.083 UP > FES	< 0.001 LP > FES
Shrub sapling species richness	0.15 0.13 (0.08)	0.373	< 0.001 LP > FES
Tree sapling height	4.25 3.93 (1.18)	0.005 FES > UP	0.012 LP > FES
Shrub sapling height	2.40 2.32 (1.38)	0.282	< 0.001 LP > FES

CHAPTER 5
GENERAL DISCUSSION

Our study of forest regeneration in Kibale National Park, Uganda, has advanced our knowledge of the complex processes of tropical forest succession. Given the extent of tropical deforestation, such information will be critical for managing successional habitats to enhance forest regrowth. We have shown that understanding plant-animal and plant-plant interactions will be important to managing successional habitat to speed forest regrowth. We also evaluated several restoration strategies using timber plantations to facilitate forest succession. Below we summarize our main results and management recommendations for each chapter.

In Chapter 2 we explored the importance of plant-animal interactions in determining successional patterns. Specifically, we studied the impact of animal mediated seed dispersal to forest succession in sites differing in initial recruit availabilities. Our main findings and subsequent management recommendations are as follows:

1. Post-disturbance animal-mediated seed dispersal increased recruitment of tree seedlings during forest succession. When animal-mediated seed dispersal is low, managers should consider encouraging it.
2. Seed dispersal was more important to succession where initial on-site recruit densities were low than it was where initial on-site recruit densities were high. This differential influence enabled forest structure in successional habitats

with low initial recruit availabilities to match that in successional habitats with high initial recruit availabilities within six years. To avoid unnecessary interventions, managers should try to anticipate when sites differing in initial recruit availability will converge in forest structure.

3. In all successional habitats, seedling recruitment of animal-dispersed trees was establishment limited, not dispersal limited. In similar situations, managers should consider improving the understory environment for seedling establishment (e.g., opening the canopy to increase understory light).
4. Tree seedling recruitment patterns were complex, fluctuating through time and differing among successional habitats. Because such patterns can make accurate predictions difficult, managers should consider using multiple strategies for enhancing seed dispersal and seedling recruitment.
5. Early in succession, seed-dispersing birds had a greater impact on seedling recruitment than did seed-dispersing mammals. Thus, attempts to encourage seed rain early in succession may be most successful when targeting birds, not mammals.

In Chapter 3 we explored the influence of plant-plant interactions (competition and facilitation) during forest succession in logged plantations. Specifically, we examined how shrubs and other vegetation impact tree recruitment, growth, and survival in successional habitats varying in initial on-site recruit availabilities. First, we looked for important interactions during succession with a correlative analysis of variables describing the structure and composition of the tree and shrub community. Subsequently, we removed shrubs and all

non-tree vegetation from plots to determine the effect removal had on trees. As we have seen in Chapter 1, our results revealed that successional processes are complex and can make successful interventions difficult.

1. The correlative analysis of successional habitats showed that relationships between trees and shrub, and seedlings and saplings were variable. Thus, managers should be cautious about basing interventions on simple assumptions about plant community interactions.
2. However, plant interactions were less variable in the successional habitat with lower initial on-site recruit density, suggesting that interventions may be more successful/predictable where recruit densities are lower.
3. In experimental manipulations where we removed shrubs or all non-tree vegetation, we saw little effect on tree recruitment, growth, or survival at the community level. However, many species showed a significant response (positive or negative) to treatments, suggesting that manipulations may be most successful when targeting specific species, not the entire community.
4. Based on trends from our experiments and results from the literature, we suggest that managers may successfully promote seedling establishment and growth by planting or retaining a nurse crop of tall vegetation. In contrast, sapling survival and growth may be best promoted by removing adjacent stems that may be competing with them for resources.
5. Manipulations should favor mid- and late-successional species over early-successional species since mid- and late-successional species tend to be rare in young secondary forests.

6. Finally, because plant interactions during succession are complex, managers should expect some of their manipulations to fail. Thus, they need to be adaptable and creative with alternative strategies.

In Chapter 4 we explored the use of timber plantations to restore natural forests on degraded tropical lands. This strategy has received considerable attention from restoration ecologists in the last few years. However, few studies have considered effects of timber harvest on forest succession, or compared using plantations to alternative strategies. In this study we examined the influence of initial on-site recruit availability on forest development, the effect of timber harvesting on succession, ways to accelerate forest regrowth, and how several restoration strategies that use plantations compare among themselves and to an alternative strategy, fire exclusion.

1. Plantations often vary in the quantity of native stems that have recruited in their understory. We found this variation led to divergent successional trajectories in two types of logged plantations. However, due to high tree recruitment rates, these trajectories began to converge within six years of logging. Managers should consider how logging in different plantation types will affect forest succession and find ways to promote succession in plantations starting with fewer native stems.
2. Removal of the timber overstory accelerated forest succession relative to unlogged plantations. Thus, timber harvest may not conflict with the goals of promoting natural forest succession.

3. While harvest accelerated forest succession, many native stems were killed or severely damaged during logging. Much of this mortality and damage was inflicted as felled timber was removed from the site. To facilitate regeneration, managers should find ways to fell and extract timber that minimize killing and damaging native stems.
4. Various strategies to enhance forest succession were attempted. Two years of removing non-tree vegetation in recently logged plantations did not enhance tree establishment, growth, or survival, suggesting that thinning treatments at the community level may not help forest regrowth in early successional habitats.
5. Leaving standing, dead timber trees as perches for seed-dispersing birds led to increased seedling establishment relative to control areas. However, though recruitment may spread away from such perches, it may be many years before large areas are affected.
6. Mortality and growth were similar among 17 seedling species planted into < 1-year-old and 6-year-old successional habitats. While this suggested that the timing of seedling planting is not important during the first years of succession, nine species did survive better in one treatment or the other.
7. Among the possible restoration strategies we evaluated, leaving timber unfelled, felling and removing timber, or felling and leaving timber in place were increasingly beneficial for promoting forest succession. However, fire-exclusion appeared to promote forest succession better than did any of these strategies.

Throughout these investigations, our tactic has been to study natural processes and use the knowledge gained to design strategies stimulating forest regrowth. Many important questions would benefit from this approach. For example, how do successional processes change as forests mature, and what are resulting management implications? Or, how do successional processes and optimal management strategies vary across gradients in disturbance intensity or resource availability? This integration of theory and application, as seen in our studies, will be needed to answer such questions and ensure the success of tropical restoration ecology.

LIST OF REFERENCES

Adedeji, F. O. 1984. Nutrient cycles and successional changes following shifting cultivation practice in moist semi-deciduous forests in Nigeria. Forest Ecology and Management **9**:87-99.

Aide, T. M. and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecology **2**:219-229.

Aide, T. M., J. K. Zimmerman, M. Rosario and H. Marcano. 1996. Forest recovery in abandoned cattle pasture along an elevational gradient in northeastern Puerto Rico. Biotropica **28**:537-548.

Ashton, P. M. S., S. Gamage, I. Gunatilleke and C. V. S. Gunatilleke. 1998. Using Caribbean pine to establish a mixed plantation: testing effects of pine canopy removal on plantings of rain forest tree species. Forest Ecology and Management **106**:211-222.

Berkowitz, A. R., C. D. Canham and V. R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology **76**:1156-1168.

Bertness, M. D. and R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution **9**:191-193.

Borhidi, A. 1988. Vegetation dynamics of the savannization process on Cuba. Vegetatio **77**:177-183.

Brokaw, N. V. L. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. Tropical Ecology **24**:194-200.

Brown, S. 1993. Tropical forests and the global carbon cycle: the need for sustainable land-use patterns. Agriculture, Ecosystems and Environment **46**:31-44.

Brown, S. and A. E. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology **6**:1-32.

Brown, S. and A. E. Lugo. 1994. Rehabilitation of tropical lands: a key to sustaining development. Restoration Ecology **2**:97-111.

Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology **78**:1958-1965.

Chapman, C. A. and L. J. Chapman. 1996. Exotic tree plantations and the regeneration of natural forests in Kibale National Park, Uganda. Biological Conservation **76**:253-257.

Chapman, C. A. and L. J. Chapman. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. Conservation Biology **13**:1301-1311.

Chapman, C. A., L. J. Chapman, W. Wrangham, D. Kennard and A. E. Zanne. 1999. Patterns in fruiting and flowering phenology at two sites in Kibale National Park, Uganda. Journal of Tropical Ecology **15**:180-211.

Chapman, C. A., L. J. Chapman, A. E. Zanne and M. Burgess. in press. Does weeding promote regeneration of an indigenous tree community in felled pine plantations in Uganda? Restoration Ecology.

Chapman, C. A. and J. E. Lambert. 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. American Journal of Primatology **50**:169-185.

Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. Vegetatio **66**:119-135.

Chazdon, R. L. 1994. The primary importance of secondary forests in the tropics. Tropinet **5**:1.

Da Silva, J. M. C., C. Uhl and G. Murray. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conservation Biology **10**:491-503.

Dalling, J. W. and J. S. Denslow. 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. Journal of Vegetation Science **9**:669-678.

De Rouw, A. 1993. Regeneration by sprouting in slash and burn rice cultivation, Tai rain forest, Cote d'Ivoire. Journal of Tropical Ecology **9**:387-408.

De Rouw, A. 1994. Effect of fire on soil, rice, weeds and forest regrowth in a rain-forest zone (Cote-Divoire). Catena **22**:133-152.

Denslow, J. S. and S. Guzman. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. Journal of Vegetation Science **11**:201-212.

Duncan, R. S. and C. A. Chapman. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecological Applications **9**:998-1008.

Duncan, R. S. and V. E. Duncan. 2000. Forest succession and distance from forest edge in an Afro-tropical grassland. Biotropica **32**:33-41.

Eggeling, W. J. and I. R. Dale. 1952. The indigenous trees of the Uganda Protectorate. Government of Uganda Printer, Entebbe, Uganda.

Ewel, J. J. 1980. Tropical succession: manifold routes to maturity. Biotropica **12**:2-7.

Ewel, J. J. 1986. Designing agricultural ecosystems for the humid tropics. Annual Review of Ecology and Systematics **17**:245-271.

FAO. 1999. State of the world's forests. Food and Agriculture Organization of the United Nations, Rome.

Fenner, M. and K. Kitajima. 1999. Seed and seedling ecology. in F. I. Pugnaire and F. Valladares. Handbook of functional plant ecology. Marcel-Pekken, New York.

Fernandes, D. N. and R. L. J. Sanford. 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. Conservation Biology **9**:915-922.

Fimbel, R. A. and C. C. Fimbel. 1996. The role of exotic conifer plantations in rehabilitating degraded forest lands: a case study from the Kibale Forest in Uganda. Forest Ecology and Management **81**:215-226.

Finegan, B. 1984. Forest succession. Nature **312**:109-114.

Finegan, B. 1992. The management potential of neotropical secondary lowland rain forest. Forest Ecology and Management **47**:295-321.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forest: the first 100 years of succession. Trends in Ecology and Evolution **11**:119-124.

Foster, S. A. and C. H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology **66**:773-780.

Garciamontiel, D. C. and F. N. Scatena. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto-Rico. Forest Ecology and Management **63**:57-78.

Geldenhuys, C. J. 1997. Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. Forest Ecology and Management **99**:101-115.

Gillespie, T. W., A. Grijalva and C. N. Farris. 2000. Diversity, composition, and structure of tropical dry forests in Central America. Plant Ecology **147**:37-47.

Grace, J. B. 1991. A clarification of the debate between Grime and Tilman. Functional Ecology **5**:583-587.

Graham, C. H., T. C. Moermond, K. A. Kristensen and J. Mvukiyumwami. 1995. Seed dispersal effectiveness by two bulbuls on *Maesa lanceolata*, an African montane forest tree. Biotropica **27**:479-489.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, New York.

Guariguata, M. R. 1999. Early response of selected tree species to liberation thinning in a young secondary forest in northeastern Costa Rica. Forest Ecology and Management **124**:255-261.

Hamilton, A. 1991. A field guide to Ugandan forest trees. Makerere University Press, Kampala, Uganda.

Hau, C. H. 1997. Tree seed predation on degraded hillsides in Hong Kong. Forest Ecology and Management **99**:215-221.

Holl, K. D. 1998a. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restoration Ecology **6**:253-261.

Holl, K. D. 1998b. Effects of above- and below-ground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. Forest Ecology and Management **109**:187-195.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica **31**:229-242.

Holl, K. D. and M. Kappelle. 1999. Tropical forest recovery and restoration. Trends in Ecology and Evolution **14**:378-379.

Holmgren, M., M. Scheffer and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology **78**:1966-1975.

Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201-228.

Kammesheidt, L. 1999. Forest recovery by root suckers and above-ground sprouts after slash-and-burn agriculture, fire and logging in Paraguay and Venezuela. Journal of Tropical Ecology **15**:143-157.

Katende, A. B., A. Birnie and B. Tengnas. 1995. Useful trees and shrubs for Uganda: identification, propagation, and management for agricultural and pastoral communities. Regional Soil Consultants Unit, Nairobi, Kenya.

Keenan, R., D. Lamb, O. Woldring, T. Irvine and R. Jensen. 1997. Restoration of plant biodiversity beneath tropical tree plantations in Northern Australia. Forest Ecology and Management **99**:117-131.

Kingston, B. 1967. Working plan for Kibale and Itwara Central Forest Reserves. Ugandan Forestry Department, Entebbe, Uganda.

Kuusipalo, J., G. Adjers, Y. Jafarsidik, A. Otasmo, K. Tuomela and R. Vuokko. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. Journal of Vegetation Science **6**:205-210.

Lamb, D. 1998. Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. Restoration Ecology **6**:271-279.

Lambers, H., F. S. Chapin III and T. L. Pons. 1998. Plant physiological ecology. Springer-Verlag Inc., New York.

Lang Brown, J. R., and J.F. Harrop. 1962. The ecology and soils of the Kibale grasslands, Uganda. East African Agricultural and Forestry Journal **April**:264-272.

Leslie, A. J. 1999. For whom the bell tolls. Tropical Forest Update **9**:13-15.

Levey, D. J. 1986. Methods of seed processing by birds and seed deposition patterns. 147-158 in A. Estrada and T. H. Fleming. Frugivory and seed dispersal. Dr. W. Junk Publishers, Dordrecht.

Li, X. D. and S. D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology **79**:2694-2705.

Li, X., S. D. Wilson and Y. Song. 1999. Secondary succession in two subtropical forests. Plant Ecology **143**:13-21.

Lowry, R. (2000). VassarStats: Website for Statistical Computation, Vassar College. **2000**.

Lugo, A. E. 1992. Tree plantations for rehabilitating damaged forest lands in the tropics. 247-255 in M. K. Wali. Ecosystem rehabilitation, Volume 2: Ecosystem analysis and synthesis. SPB Academic Publishing, The Hague, The Netherlands.

Lugo, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. Forest Ecology and Management **99**:9-19.

Nepstad, D. C., C. Uhl, C. A. Pereira and J. M. C. Da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos **76**:25-39.

Nepstad, D. C., C. Uhl and E. A. S. Serrao. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio **20**:248-255.

Osmaston, H. A. 1959. Working plan for the Kibale and Itwara forests: period 1959-1965. Government of Uganda Printer, Entebbe.

Otsamo, R. 1998. Effect of nurse tree species on early growth of *Anisoptera marginata* Korth. (Dipterocarpaceae) on an *Imperata cylindrica* (L.) Beauv. grassland site in south Kalimantan, Indonesia. Forest Ecology and Management **105**:303-311.

Otsamo, R. 1998. Removal of *Acacia mangium* overstorey increased growth of underplanted *Anisoptera marginata* (Dipterocarpaceae) on an *Imperata cylindrica* grassland site in South Kalimantan, Indonesia. New Forests **16**:71-80.

Otsamo, R. 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. New Forests **19**:69-93.

Parrotta, J. A. 1993. Secondary forest regeneration on degraded tropical lands: the role of plantations as "foster ecosystems." 63-73 in H. Lieth and M. Lohmann. Restoration of tropical forest ecosystems. Kluwer Academic Publishers, The Netherlands.

Parrotta, J. A. 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. Journal of Vegetation Science **6**:627-636.

Parrotta, J. A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. Forest Ecology and Management **124**:45-77.

Parrotta, J. A. and O. H. Knowles. 1999. Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecology **7**:103-116.

Parrotta, J. A., J. W. Turnbull and N. Jones. 1997. Introduction - Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**:1-7.

Pickett, S. T. A. and M. J. McDonnell. 1989. Changing perspectives in community dynamics: a theory of successional forces. Trends in Ecology and Evolution **4**:241-245.

Pinard, M., B. Howlett and D. Davidson. 1996. Site conditions limit pioneer tree recruitment after logging of dipterocarp forests in Sabah, Malaysia. Biotropica **28**:2-12.

Pinard, M. A., M. G. Barker and J. Tay. 2000. Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. Forest Ecology and Management **130**:213-225.

Pohill, R. M. 1952. Flora of tropical East Africa. A.A. Balkema, Rotterdam.

Powers, J. S., J. P. Haggar and R. F. Fisher. 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. Forest Ecology and Management **99**:43-54.

Putz, F. E. and C. D. Canham. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. Forest Ecology and Management **49**:267-275.

Raffaele, E. and T. T. Veblen. 1998. Facilitation by nurse shrubs of resprouting behavior in a post- fire shrubland in northern Patagonia, Argentina. Journal of Vegetation Science **9**:693-698.

Rogers, H. M. and A. E. Hartemink. 2000. Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea. Journal of Tropical Ecology **16**:243-251.

Saldarriaga, J. G., D. C. West, M. L. Tharp and C. Uhl. 1988. Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. Journal of Ecology **76**:938-958.

Sivell, D., T. Lee and L. Stewart. 1996. Frontier-Uganda baseline surveys of wildlife protected areas. Technical report # 8: Kibale National Park - grassland survey. Ministry of Natural Resources and International Union for the Conservation of Nature, Kampala.

SPSS (1999). SPSS 10.0.5 for Windows. Chicago.

Sun, D. and G. R. Dickinson. 1996. The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical north Australia. Biotropica **28**:272-276.

Sun, D., G. R. Dickinson and A. L. Bragg. 1995. Direct seeding of *Alphitonia petriei* (Rhamnaceae) for gully revegetation in tropical northern Australia. Forest Ecology and Management **73**:249-257.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. American Naturalist **125**:827-852.

Tilman, D. 1990. Constraints and tradeoffs-toward a predictive theory of competition and succession. Oikos **58**:3-15.

Toh, I., M. Gillespie and D. Lamb. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. Restoration Ecology **7**:288-297.

Toriola, D., P. Chareyre and A. Buttler. 1998. Distribution of primary forest plant species in a 19-year old secondary forest in French Guiana. Journal of Tropical Ecology **14**:323-340.

Tucker, N. I. J. and T. M. Murphy. 1997. The effects of ecological rehabilitation on vegetation recruitment: some observations from the wet tropics of North Queensland. Forest Ecology and Management **99**:133-152.

Uhl, C. 1982. Recovery following disturbances of different intensities in the Amazon rain forest of Venezuela. Interciencia **7**:19-24.

Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. Journal of Ecology **75**:377-407.

Uhl, C., R. Buschbacher and E. A. S. Serrao. 1988. Abandoned pastures in eastern Amazonia I. Patterns of plant succession. Journal of Ecology **76**:663-681.

Uhl, C., H. Clark and K. Clark. 1982a. Successional patterns associated with slash-and-burn agriculture in the Upper Rio Negro region of the Amazon basin. Biotropica **14**:249-254.

Uhl, C., K. Clark, H. Clark and P. Murphy. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. Journal of Ecology **69**:631-649.

Uhl, C., C. Jordon, K. Clark, H. Clark and R. Herrera. 1982b. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. Oikos **38**:313-320.

Uhl, C. and J. B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the Eastern Amazon. Ecology **71**:437-449.

Uhl, C., J.B. Kauffman and D. L. Cummings. 1988. Fire in the Venezuelan Amazon 2: environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. Oikos **53**:176-184.

van Perlo, B. 1995. Birds of eastern Africa. Harper Collins Publishers, London.

Vieira, I. C. G., C. Uhl and D. Nepstad. 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. Vegetatio **115**:91-99.

Walker, L. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. Journal of Vegetation Science **5**:525-532.

Williams, J. G. and N. Arlott. 1980. Birds of East Africa. Harper Collins Publishers, London.

Williams-Linera, G. and J. J. Ewel. 1984. Effect of autoclave sterilization of a tropical andept on seed germination and seedling growth. Plant and Soil **82**:263-268.

Zahawi, R. A. and C. K. Augspurger. 1999. Early plant succession in abandoned pastures in Ecuador. Biotropica **31**:540-552.

Zanne, A. E. and C. A. Chapman. in press. Expediting forest regeneration in tropical grasslands: distance and isolation from seed sources in plantations. Ecological Applications.

Zimmerman, D. A., D. A. Turner and D. J. Pearson. 1996. Birds of Kenya and northern Tanzania. Princeton University Press, Princeton.

BIOGRAPHICAL SKETCH

I was born (19 December 1969) and raised in Gulf Breeze, Florida. Near the time of my birth, my parents (Robert A. and Lucy R. Duncan) became avid birdwatchers. Their contagious enthusiasm for birding and interest in conservation spread to me and my younger brother (William W. Duncan). After high school, I attended Eckerd College in St. Petersburg, Florida, where I earned a BS degree in biology. During these years, a field course and several research assistantships in Central America piqued my interest in tropical forest ecology and conservation. I pursued these interests by earning my MS degree in zoology with Dr. Colin Chapman at the University of Florida. This work took me to Kibale National Park, Uganda, where I continued working in pursuit of my PhD. After graduating I will continue to pursue my interests in research, conservation, and teaching.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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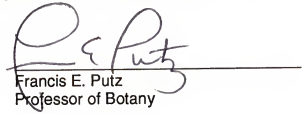
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Education.

May 2001

Dean, Graduate School